PSYCHOLOGICAL AND PHYSIOLOGICAL PROCESSES UNDERLYING PERCEPTION AND ATTENTION: A STUDY OF BINOCULAR RIVALRY.

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Thesis submitted for the degree of
Doctor of Philosophy in Psychology
University College London
1976

ABSTRACT

This thesis is concerned with an investigation of certain psychological and physiological processes underlying perception and attention. In this context binocular rivalry is selected for close investigation since it has at different times been related to both perception and attention. This relationship is demonstrated by a series of investigations which show that the stimulus that is currently non-dominant in rivalry is nevertheless fully analysed. The nature of rivalry indicates that two complementary visual systems contribute to perception and attention. Whilst one system (superior colliculus - posterior association cortex) is responsible for monitoring unperceived/unattended information and initiating a shift in attention, the other system (geniculo-striate cortex) is concerned with currently perceived/attended information. In the terminology of control theory, these two visual systems contribute to feedforward and feedback control respectively. The interaction between the two is considered to be the correlate of conscious perception and attention, reflecting the sampling of sensory information by a process that matches this information against the expectations based on a model of the world. Confirmation of a number of predictions refines and further anchors the theory to physiological mechanisms.

ACKNOWLEDGEMENTS

The author is indebted to Dr. N.F. Dixon for serving as a most helpful and encouraging supervisor, and for revealing the pleasures to be had from researching in psychology. The author would also like to thank the following: Dr. A.R. Jonckheere for advice on statistical matters; Dr. D.J. Powell for preparing the computer program used to generate the visual display in Experiment 13; the Computer Services Centre, University College London, for providing facilities for data analysis; the technical staff of the Department of Psychology for the time and energy spent in designing and constructing many items of equipment; and the Science Research Council for a Postgraduate Studentship.

Special thanks must go to Lesley and Jill, who suffered extended periods of boredom during the preparation of this thesis.

CONTENTS

INTRODUCTION

CHAPTER 1 BINOCULAR RIVALRY: A CONTEXT FOR THE INVESTIGATION OF PERCEPTION AND ATTENTION

1.1 Introduction: The Significance of Subliminal Perception for Perception and Attention

In view of the renewed credibility with which the subliminal perception hypothesis has emerged (cf. Dixon, 1971)* an investigation of the psychological and physiological processes underlying perception and attention must begin by considering the fundamental implications of the notion that there may be perception without awareness.

As important as the evidence for subliminal perception are the data which indicate that it does not merely reflect a diluted version of conscious perception (cf. Dixon, 1971). First, there are the qualitatively different effects that result from the subliminal and supraliminal presentation of a stimulus. Thus, whilst the meaning of a subliminal stimulus is the major determinant of a subject's response, it is the structural character of a supraliminal stimulus that takes precedence. Second, a subliminal stimulus is much more potent when presented quite a way below threshold than when presented near to threshold. Third, the processes involved in subliminal perception, despite the second observation, are not solely concerned with "diluted" stimuli which fall below some perceptual threshold. Such facts indicate that the processes underlying subliminal perception are quite different from those that are more directly responsible for mediating conscious perceptual experience. This not only adds to the credibility of the subliminal perception hypothesis, by avoiding the illogicality of having a functional replication of the perceptual process, once at an unconscious and once at a conscious level, but suggests that an understanding of subliminal perception will help to isolate those processes that are responsible

* cf. also, Erdelyi (1974)

for conscious perceptual experience. In this way subliminal perception has the most direct implications for theories of perception.

The fact that a subject may respond to the meaning of a subliminal stimulus indicates that perception reflects something other than the central nervous system's encoding or analysis of the sensory information. Because of this, the notion of subliminal perception proves difficult for theories that are based on the premise that perception simply, "passively" reflects the underlying analysis of sensory information. Thus, Neisser (1967), for whom the processes by which stimulus structure and meaning are determined are themselves in consciousness, prefers not to accept the notion of perception without awareness. Much less troubled by subliminal perception however, is the category of theory which considers perception to reflect "active" processes. MacKay (1967), for example, believes that perception reflects a matching, or hypothesis-testing process, that is undertaken partly on the basis of the results of the analysis of sensory information. Since perception is thus considered to be something over and above the encoding processes, this theory is quite able to accommodate subliminal perception. It could be assumed, for example, that a stimulus may not contribute to conscious perceptual experience because it is not sampled by the matching process (cf. Chapter 6 below).

In view of the close relationship between perception and attention, subliminal perception has similar implications for theories of selective attention. That there is a relatioship is obvious; we perceive those things to which we attend, and we can be said to be attending to those things currently being perceived. Indeed, this last point was an

implicit criteria in the selection of an experimental paradigm for the study of selective attention. Thus, the feature of the dichotic listening and shadowing paradigm that most recommended it for this purpose, was the fact that most of the non-attended (non-shadowed) information was not consciously perceived by the subject. The close relationship between perception and attention has recently been made more explicit (Lewis, 1970; Corteen and Wood, 1972; MacKay, 1973; Posner and Klein, 1973). As we shall see in a later chapter, there are physiological data which confirm this close relationship. For example, the late components of the cortically evoked potential have been associated with both attention and conscious perceptual experience.

Mirroring the passive theories of perception are those theories of selective attention that are based on the premise that there exists a one-to-one relationship between the analysis of, and attention towards, a stimulus. In the same way that the former postulate processes which prevent the analysis of information when this goes unperceived, so the passive theories of attention assume the existence of comparable processes that prevent attention from being focused on unimportant information. Broadbent (1958), for example, whose model of attention clearly belongs to this category, incorporates a peripherally acting filter to prevent anything but a primitive analysis of unattended information. Interestingly, and consistent with the implicit assumption of a one-to-one relationship between the analysis of, perception of, and attention towards a stimulus, those features of the unattended message that are perceived are presumed to be analysed before the focus of action of the filter. The implications of subliminal perception for

theories of attention are, then, the same as for theories of perception: they need not incorporate suppressive or inhibitory processes that prevent non-attended information from being fully analysed (cf. Deutsch and Deutsch, 1963).

This, then, is the significance of subliminal perception. The phenomenon indicates that active processes, over and above the analysis of sensory information, are directly responsible for conscious perceptual experience/attention, and it is with an attempt to illuminate these processes that the present thesis is concerned. Special consideration is given to physiological factors in the belief that to provide a physiological interpretation may be the optimum way of defending and extending the active approach to perception and attention. Moreover, recourse to physiological parameters provides a context in which to bring together data from studies of attention and perception. This is particularly important since the two phenomena have in general been investigated in quite different contexts. Also with this cross-fertilization in mind, a "boundary" phenomenon, that has at different times been thought to reflect processes fundamental to both perception and attention, was selected for experimental investigation.

Qualifying as a boundary phenomenon is binocular rivalry. However, this qualification is not the only feature to recommend its investigation. It has been argued that perception and attention reflect processes over and above those analytic processes involved in subliminal perception. Ideal, therefore, is a situation that simultaneously involves a stimulus that is perceived and a stimulus that, though capable of being perceived, and though fully analysed, does not contribute to perceptual experience. Comparing the different treatment that such stimuli are accorded would

then isolate the active processes of conscious perception. If it could be shown that binocular rivalry reflects "central" or active processes, with the non-dominant stimulus being fully analyzed, then it would provide this ideal situation. It is important, therefore, that binocular rivalry should be shown to be a context for subliminal perception.

To summarize, it is argued that the processes underlying subliminal perception are distinct from those more directly responsible for mediating conscious perception and attention, and that, therefore, the latter phenomena reflect processes over and above the analysis of sensory information. A better understanding of such active processes will, it is argued, benefit from comparing data from studies of perception and attention, whilst making full use of the bridging concepts of physiology. To this end, it is suggested that it would be most appropriate to investigate a "boundary" phenomenon that may be considered as either perceptual or attentional, and that involves stimuli of which the subject is unaware. Whilst binocular rivalry is suggested for the purpose, it is appreciated that it must first be demonstrated that the perceptual suppression that it involves does not reflect the inhibition or blocking of sensory information at or before the stage at which the stimulus is successfully analyzed.

1.2 Content of Major Sections

Part 1

Since the significance of binocular rivalry hinges upon the notion that the perceptual suppression that it involves does not reflect the blocking or inhibition of sensory information at or before the stage at which stimuli are analyzed, Part 1 of this thesis directs itself at this problem. Several investigations are reported which demonstrate that whilst a monocular stimulus is phenomenally suppressed it continues to be analyzed by the visual system. This supports the conclusion drawn from a critical review of the literature and confirms the notion that binocular rivalry involves subliminal perception.

Part 2

The data from these investigations go some way to identifying the physiological mechanisms involved in the phenomenon, and in Part 2, what is known of the contribution of these mechanisms to perceptual experience and attention is considered. Accordingly, the outline of a model of perception and attention is described that incorporates the notion that there are two visual systems.

Part 3

There is an attempt in Part 3 to test and refine the theoretical notions developed in Part 2. Thus, it is suggested that since the processes responsible for binocular rivalry are central processes, they should not be critically dependent upon the mode of stimulus presentation. A series of investigations reveals that the processes involved in rivalry also contribute to other perceptual phenomena. Thus, for example, it is demonstrated that the processes underlying the phenomena associated with stabilized images are akin to those underlying binocular rivalry. These

investigations also suggest how the theoretical notions of Part 2 may be developed and refined, and a number of small scale investigations offer preliminary tests of these suggestions. There follows a discussion of the experiments that have been published in the interim, between the planning of the experiments reported herein and the preparation of this manuscript. The results of these experiments are shown to offer good support for the theoretical notions developed in Part 2. Finally, this section, and the thesis, concludes with suggestions for further research.

1.3 Practical Considerations

Before entering Part 1, a number of practical matters require consideration. First, since the thesis is as much a theoretical as an empirical study, the theoretical discussions are not reserved until the final sections of the thesis. Rather, matters of theory are discussed as they arise from consideration of empirical observations. Second, since it is one of the aims of the investigations reported in Part 1 to demonstrate that the perceptually "suppressed" information in rivalry is not in any real sense suppressed or blocked, the term becomes rather innappropriate. However, it has been used extensively in the past, and reads much easier than the more precise term "non-dominant", so that in those places where the author wishes to take care in his discussion, the more cumbersome term "non-dominant" is employed, whilst, when precision is less important, the more obvious term "suppressed" is employed. Third, although binocular rivalry traditionally incorporates the alternations in perceptual dominance of the two monocular fields, included under the same term are those phenomena that result from conditions of dichoptic presentation wherein only one of the alternatives is ever perceived, as for example, when stimulus exposure duration is brief. Until such time as the processes involved in the two situations are shown to be fundamentally different, they will be considered together. In defence of this tactic, it has generally been found that those factors which predispose towards the dominance of a particular stimulus when rivalry alternations are allowed to occur, also predispose towards favouring the same stimulus when the conditions of presentation preclude the perception of both.

PART 1

THE FATE OF SUPPRESSED INFORMATION IN BINOCULAR RIVALRY

CHAPTER 2 CRITICAL REVIEW OF THE LITERATURE

2.1 Analysis of current approaches

2.1.1 Introduction

Although data are to be reviewed in the following sections that offer support for the hypothesis that there is continuous analysis of a stimulus despite its suppressed status in rivalry, it will be useful to anticipate whether such evidence will necessarily conflict with any of the existing theoretical approaches toward the phenomenon, with the data upon which these are based, or with the general context against which the phenomenon must be viewed. In this section it is asked whether, as is suggested by the possibility of exerting voluntary control over the course of rivalry, the literature indicates that the phenomenon reflects 'central' processes rather than a direct mutual interaction between the two monocular channels based on reciprocal inhibition and adaptation. In addition, since the facts relating to binocular rivalry must have implications for theories of stereopsis, it is also asked how the hypothesis that there is a continuous analysis of suppressed information fits in with these theories and the facts upon which they are based. Finally, it is argued that although rivalry may involve rather central processes, peripheral factors may nevertheless make their contribution.

2.1.2 Voluntary control over rivalry

The observations of William James (1890), Breese (1899), Sherrington (1906), MacDougall (1906) and Helmholtz (1911), persuaded them to assign a central place to binocular rivalry in their discussions of attention, the implication being that rivalry involves central processes, rather than peripheral or sensory ones. Thus, Breese (1899) and Helmholtz (1911) discovered that it was possible for an observer to exert some control over the course of rivalry even to the extent of being able to avoid the suppression of one of the monocular fields. Therefore, although bright and distinct objects in one field generally prevail over those which are weaker and presented within the contralateral field, the trend may be reversed by directing attention toward the latter. The critical factor for Helmholtz appeared to be that the observer should have a 'definite purpose in mind' in relation to one of the stimuli. Thus, the different elements in one of the fields should be counted or compared in some way. For example, these two authors, when presenting their subject with differently oriented grid patterns to the two eyes, could ensure that one or the other grid dominated perceptually by instructing him to count the lines within a particular grid, or compare the spaces between the lines. Similarly, when a sample of text was presented to one eye and a picture or map was presented to the other, reading the former, or studying the latter, encouraged the continued dominance of the appropriate field. As might be anticipated from this, when a different sample of text was presented to each eye (a situation analogous to the dichotic listening paradigm), it was possible to read one of these (shadow?) successfully, providing that there was some physical characteristic that distinguished them. Presumably, in this case there is little perceptual interference from the text being ignored.

Primarily, because of this voluntary control over rivalry,

Helmholtz concluded that 'the content of each separate field comes to consciousness without being fused with that of the other field by means of organic mechanisms; .... the fusion of the two fields in one common image, when it does occur, is a psychic act'. Thus, Helmholtz went further than the other authors and suggested that the fact of voluntary control was evidence that both monocular stimuli were fully analysed, regardless of whether one was suppressed or both were fused into a single percept.

For these authors then, the discovery that some control could be exerted over the course of rivalry pointed to the rather central nature of the underlying processes. It is important, therefore, that others have more recently confirmed these findings (Collyer and Bevan, 1970; Lack, 1969; Meredith and Meredith, 1962), and have demonstrated that this control is not mediated by peripheral responses. Thus, Lack (1971) tested for the possible role of fluctuations in accommodation in the voluntary control of rivalry. Finding that neither adopting artificial pupils nor paralyzing the intrinsic muscles of the eyes affected the degree of control, and that the subjects could even exert some control over rivalling after-images, Lack concluded that accommodation changes could not make a significant contribution. However, a number of earlier studies, cited by Lack (1971), were thought to have provided evidence to the contrary. Thus, MacDougall (1903) paralyzed the intrinsic muscles of his left eye and observed the increased predominance of the right field*. This increase could, however, easily be contradicted by directing attention to the other field, and indeed, MacDougall's thesis is that peripheral factors are not a prerequisite for control over rivalry. George (1936) discusses similar effects of eye paralysis, but fails to report his data or the results of a statistical test. Finally, rather more convincing evidence, superficially at least, for the involvement of accommodation changes, was presented by Fry (1936). There are several points of criticism, however, that may be directed at this study. First, Fry states that paralyzing the

* right eye field

intrinsic muscles of the subjects precluded any voluntary control over the rivalry state, yet the data that are presented in his report show this not to be the case. There is clear evidence for a residual degree of control, despite paralysis. Secondly, there is an inconsistency in the report. Whilst Fry concludes that a change in accommodation is the critical factor in the control of rivalry between normally-viewed images, he concluded that changes in interocular pressure must mediate the voluntary control over rivalling after-images. Moreover, this last conclusion is simply based upon the demonstration that externally-applied pressure to the eyeball serves to influence the rivalry between contralateral after-images. Clearly this demonstration does not warrant the conclusion drawn by Fry. Thirdly, and importantly, Fry's results are inconsistent with the effect that blurring an image (which is presumed to be the critical factor in fluctuating accommodation) is now known to have on rivalry (Levelt, 1966). Thus, whilst Fry purports to have demonstrated that subjects can voluntarily accelerate the rate of rivalry alternation, Levelt (1966) has shown that defocussing either one or both rivalling images serves only to decrease the rate of alternation.

It is clear, therefore, that Fry's data simply do not justify the conclusion he offers. Moreover, whilst it is conceivable that changes in accommodation might affect the overall rate of alternation, it is difficult to imagine how they might give rise to an increased predominance of one stimulus over the other, since there seems to be no evidence that the state of accommodation may be different for the two eyes (Personal Communication, F M Toates, 1975).

In summary, the possibility of exerting a degree of control over rivalry not only implicates rather central processes in the phenomenon but also, for Helmholtz, offers proof that the two monocular fields remain independent, with the information within each being fully analyzed, regardless of the state of dominance. The fact that peripheral factors do not play a

significant part in the control is consistent with this. These findings then, are consistent with the thesis that is to be developed.

2.1.3 The contribution of reciprocal inhibition and adaptation

The view that rivalry reflects a competition between the corresponding parts of the two monocular channels for individual common pathways has been encouraged by the fact that it is not difficult to conceive that the two monocular inputs are capable of preventing each other's transmission further into the visual system by a process of reciprocal inhibition. Early physiological evidence from single-cell recording of the visual system appeared to be particularly consistent with this (Jung, 1961; Bishop, 1971). If taken in conjunction with the notion that the alternating dominance of the two fields of rivalry simply reflects the successive adaptation and recovery from adaptation of the two fields (cf. Crovitz and Lockhead, 1967), rivalry would appear to reflect a passive and relatively peripheral physiological process. Evidence which suggests that reciprocal (contra-lateral) inhibition and adaptation do not, in fact, contribute to rivalry further strengthens the case for considering the potentially central nature of the phenomenon.

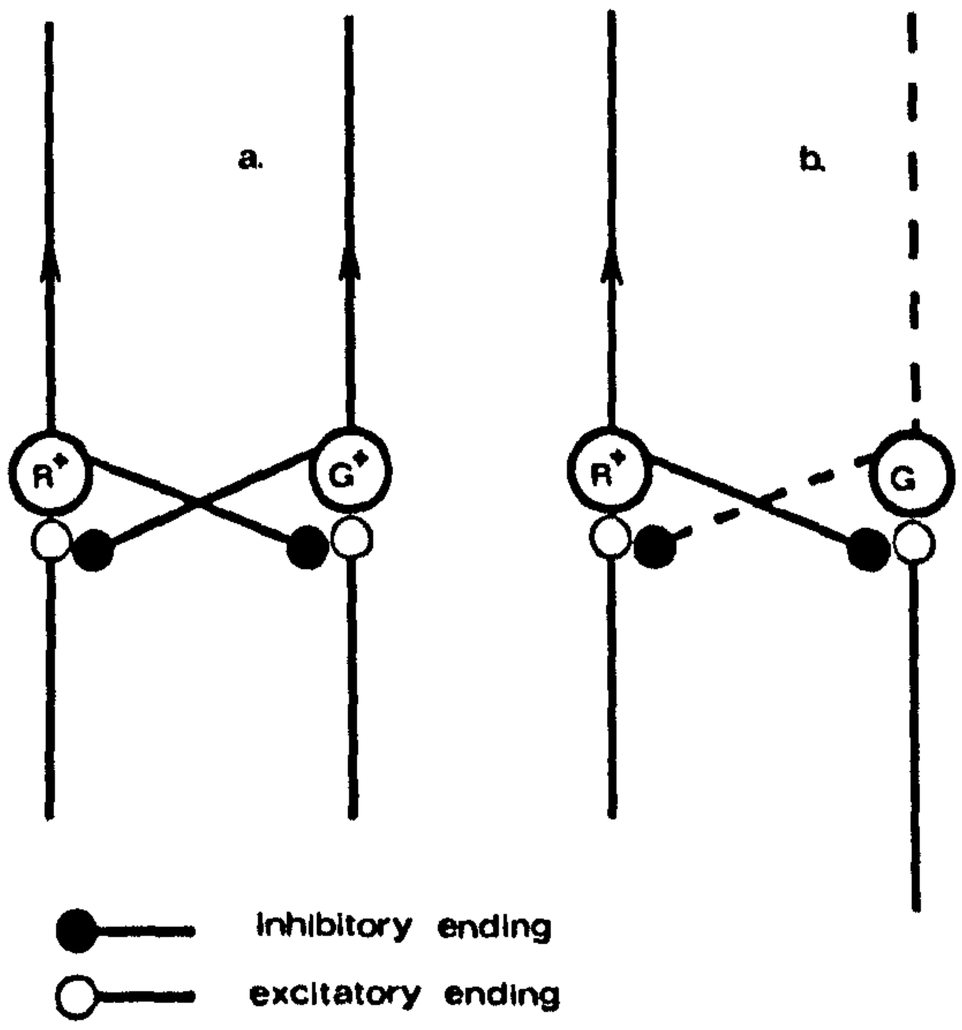
Though not designed to determine the contribution of adaptation to rivalry alternations, an early experiment by De Vries and Washburn (1909) does provide data thatare relevant to this point. Their subjects observed the rivalry between differently coloured squares and then between the complementary after-images of these squares. Some subjects were instructed to influence the course of rivalry by favouring the dominance of one of the two fields. When instructed in this way, subjects could lengthen the average dominance duration of one field and shorten the average dominance duration of the other. De Vries and Washburn failed to discover, however, a corresponding change in the phase durations of the two after-images. It would appear

from this, therefore, that the two monocular channels are equally subject to adaptation regardless of the perceptual status of the corresponding images. If rivalry alternations do reflect the successive adaptation and recovery from adaptation of the two fields, a corresponding change should have been observed in the rivalry of the after-images.

An adaptation explanation of the alternations might also predict a relationship between successive individual dominance phase durations. This is perhaps easier to envisage for rivalry between differently coloured, say red and green, homogeneous fields, the assumption being that mutual recurrent inhibitory processes exist between the corresponding neural channels. As a first approximation, a model might hold that during the suppressed phases of green, say, the corresponding neural channel, or more specifically that portion proximal to the inhibitory output emanating from the currently dominant red channel (cf. Fig 1), would be free to recover from the adaptation incurred during the preceding phases of green dominance. With the dominant red channel eventually adapting, however, these inhibitory influences would wane, allowing progressively stronger inhibitory influences to be exerted on the red channel itself until, eventually, the opponent systems in question would reverse roles. Predictable from this is the existence of a positive correlation between the durations of successive alternate red/green phases of dominance, since longer periods of red dominance, for example, would leave that channel adapted to a relatively greater extent, necessitating a longer period for recovery from adaptation and suppression. As Fox and Check (1972) point out, "variations in the initial magnitude of suppression would produce concomitant variations in the time required for its decay, and these variations in decay would correspond to variations in the durations of suppression phases. This .... would seem to be most compatible with a model of rivalry based upon reciprocal inhibition that would make assumptions about fatigue or adaptation processes to account for the shifts of

Figure 1

The type of neural network implied by the adaptation and reciprocal inhibition explanation of rivalry between chromatic stimuli (red and green). The network, a, incorporates mutual recurrent inhibitory processes between neural channels selectively sensitive to red (R^+) and green (G^+). Represented in b is the state of affairs during a dominance phase of a stimulus, with the dashed lines indicating the aspect of the neural network freed from the influence of its stimulus, and hence able to recover from its adapted state.


a.
b.
R+
G+
R+
G
inhibitory ending
excitatory ending

phenomenal state between the two eyes" (op cit p 284).

However, direct statistical tests of sequential dependency have yielded negative results (Fox and Herrman, 1967; Blake, Fox and McIntyre, 1971). Furthermore, the nature of the function that has been found to describe the frequency distribution of the rivalry phase durations reasonably well is consistent with the sequential independence of successive phases. Fox and Herrman (1967), Levelt (1967) and Blake, Fox and McIntyre (1971) have all demonstrated that a gamma function describes the distribution of dominance phase durations. In addition, Fox and Check (1972) tested a further prediction of the adaptation approach to rivalry. These authors argued that since a currently dominant stimulus suffers increasing adaptation, whilst the currently suppressed stimulus gradually recovers, the magnitude of the perceptual suppression should steadily decrease within any particular dominance phase. Fox and Check tested this prediction by determining subjects' recognition thresholds for various forms that were presented within a suppressed field, at three temporal points after the onset of suppression in this field. Finding that the recognition threshold was raised by equal amounts throughout the suppression phase, Fox and Check concluded that adaptation could not explain shifts in dominance.

Turning finally to the possible involvement of reciprocal inhibitory mechanisms in rivalry, it has been found that altering the stimulus parameters of just one rivalling field has an asymmetrical effect on the course of rivalry. Thus, Levelt (1966) and Fox and Rasche (1969) have reported that increasing the 'stimulus strength' (e g increasing the contrast) of a rivalling image causes a change in the mean duration of dominance of the contralateral image only: the mean duration of dominance of the changed stimulus remains unaffected. For the latter authors this finding contradicts a reciprocal inhibition model of rivalry, since this assumes that "suppression in one eye and dominance in the other eye both result from a single process". Thus, increasing the 'strength' of a stimulus should have the effect of

ensuring that this stimulus not only inhibits the contralateral image for extended periods, but also recovers from the inhibitory effects of this contralateral stimulus more quickly. Since their results show only the former effect, Fox and Rasche reject the notion that reciprocal inhibition contributes to suppression in rivalry.

Though these studies question the contribution of the processes of adaptation and reciprocal inhibition to rivalry, it must also be admitted that (i) a number of additional postulates are required before the type of model outlined above is capable of explaining some of the most basic features of rivalry, and before a positive correlation between successive dominance phases can be definitely predicted, and (ii) the concept of adaptation can be incorporated in a model of the alternation process (albeit in a much more indirect way) that predicts the independence of successive phase durations (cf Taylor and Aldridge, 1974, who propose such a model for the alternations of ambiguous figures). However, these experiments do illustrate that adaptation and reciprocal inhibition can not be used to explain rivalry in any direct way.

2.1.4 The complete suppression of a monocular channel

The fact that the two monocular channels remain compact, and separated from each other until some stage within visual cortex, has encouraged the notion that some form of reciprocal inhibition exists between them and has made it easy to conceive of rivalry as a passive process involving the suppression, or switching off, of all the information within one of the channels. Thus, rivalry is often regarded as a competition between the two 'eyes' and this mirrors the mistaken view that selective attention in a dichotic listening situation is mediated by the blocking or filtering of all information originating in a particular ear. However, the fact that rivalry may involve the selective suppression of different parts or aspects of the two monocular stimuli immediately reveals the inadequacy of such an approach. For example, Creed (1935), Crain (1935)[61] and Triesman (1962) have all demonstrated that when differently-coloured and differently-structured targets are presented dichoptically, the structural information from one monocular image might combine with the colour information from the contralateral field. Similarly, Reventlow (1961) has demonstrated that, although the structural information from a moving display that is presented to one eye may be suppressed, the movement itself may escape suppression and be grafted on to the dominant, contralateral image. Crain (1961); Wade (1973) and Whittle, Bloor and Pocock (1968) have also provided evidence that rivalry need not simply reflect an underlying competition or alternation between the two monocular channels. These authors demonstrate that the alternation may be between sets of lines having different orientation, even when the similarly orientated lines are distributed between the two eyes. Thus, lines having the same orientation may rival in synchrony regardless of the eye to which they are presented.

2.1.5 Rivalry and theories of stereopsis

The traditional fusion or projection field theory of stereopsis holds that stereopsis and the singleness of binocular vision result from the combining or fusing of the two monocular fields at a physiological and perceptual level. Slightly complicating the issue, the occurrence of stereopsis under Panum's limiting case, and under conditions that yield diplopia, has been taken to suggest that fusion at the latter level is somewhat independent of fusion at the former level and not a prerequisite for stereopsis. An alternative explanation, however, may be that a monocular image is capable of both combining with a contralateral image, and either giving rise to a separate image or fusing with an additional contralateral image (cf for example, Asher, 1953, Experiment 8).

Implied in these theories is the notion that both monocular fields contribute to perceptual experience and, in particular, to the perception of depth. When disparate fields combine to yield stereopsis without diplopia it is assumed that the objects in depth adopt a position in the perceptual field that is some compromise between the two monocular positions (allelatropia). It is implied, therefore, that a monocular field that suffers phenomenal (perceptual) suppression can not contribute to the perception of depth. Since the implication of this is that with the suppression of a field the analysis of its structural information is precluded, the evidence relating to these theories requires evaluation.

Offering support, Rochberg (1964) has devised stereograms, in which there is the disparity information necessary for depth, that display rivalry, and has noted that during those periods when a monocular field is totally suppressed, the impression of depth is completely lost. However, Kaufman and Pitblado (cf Hochberg, 1965) have found it difficult to replicate these original observations and have discovered that the illumination of the suppressed field requires severe reduction before

stereopsis is lost with phases of suppression. To extrapolate from such special conditions to those that involve nearly equivalent monocular stimuli is unwise. Furthermore, successful attempts have been made to demonstrate that the perception of depth which arises from retinal disparity can survive the phenomenal suppression of one of the monocular fields. Asher (1953) presents a number of stereograms that yield the impression of depth even though one of the fields may suffer suppression.[1] Similarly, Julesz (1961) has shown that when one member of a stereo-pair is apparently blurred, the binocularly-perceived image usually corresponds to the sharper member of the pair. Nevertheless, despite this suppression, the perception of depth is still obtained. More recently, Kaufman (1964a) has devised a series of stereograms to illustrate the same point. Firstly he provides evidence for the occurrence of suppression with stereograms whose monocular images are sufficiently similar for rivalry alternations not to be noticed and for the perception of depth to emerge. Secondly, as may be observed from one of the stereograms presented by Julesz (1971), Kaufman (1964a) also demonstrates that when the two monocular fields of a random-dot stereogram are differently coloured, despite the rivalry that follows, the impression of depth remains stable. Ramachandran et al (1973) have reported similar observations. Of particular importance is one of Kaufman's stereograms (Fig 5, p 399, 1964b) from which he discovered that not only did one field suppress the other but it did so immediately and continuously on presentation.

[1] Believing that the suppression of a monocular field occurs even for fields that are sufficiently similar for them to be thought capable of fusing rather than displaying rivalry, Hochberg suggests that the rivalry alternations themselves may provide the necessary information for stereopsis (cf also Livingston, 1939); Washburn, 1933, for similar theories). It has been predicted from this that those subjects which display the most rapid alternations in rivalry will also show the most efficient stereoacuity. However, although a number of authors have discovered such a correlation (eg Enoksson, 1964) the two phenomena have generally been studied in separate experimental conditions. In a well-executed study that is not subject to the same criticism, Ogle and Wakefield (1967) observed a negative correlation between the occurrence of stereopsis and rivalry.

Thus, one of the two fields never attained a state of dominance but, despite this, stereopsis was experienced. This is an important demonstration in that it eliminates explanations of the preceding demonstrations of stereopsis-despite-suppression that might suggest that some stored representation of the suppressed stimulus, made available during a preceding dominance phase of this stimulus, provides the information for stereopsis. Finally, confirming these observations in a carefully-controlled study, Ogle and Wakefield (1967) failed to find a difference in the stereoscopic threshold (stereoacuity) for rivalling and non-rivalling stimuli which carried the disparity information.

It would appear, therefore, that in attempting to determine whether perceptual fusion is a necessary condition for stereopsis, the above experiments have contradicted traditional theory and provided information that is consistent with the thesis that is to be developed. The studies demonstrate that suppressed information may be subjected to an analysis which is sufficiently rigorous to enable it to contribute to the perception of depth. Indeed, Kaufman (1964b) concludes that, for his stereograms, the experience of stereopsis represents the modification of the appearance of one monocular image by a <u>suppressed</u>, contralateral image. Consistent with this, Julesz has observed (Julesz, 1964, cf Kaufman, 1964b) that a masked stereogram may influence the perception of the immediately-succeeding masking stereogram.

Finally, in addition to providing evidence for depth-despite-suppression, Kaufman has devised a series of stereograms that contradict another aspect of the classical fusion theories of depth perception - an aspect which has encouraged the belief that a suppressed monocular field is afforded only a primitive analysis. Traditionally, stereopsis has been considered to be a result of a point-to-point matching or fusional process (Boring, 1933; Charnwood, 1951; Linksz, 1952 and, more recently, Dodwell and Engel, 1963), and as a corollary to this, rivalry suppression has been regarded as an alternative outcome of this process. Thus,

a sufficient disparity between the two monocular images prevents their fusion, with the result that access to higher centres in the brain is precluded for one of the images. Chauveau (cf Breese, 1899) maintained that when corresponding points are stimulated by different stimuli the central cells for corresponding points receive conflicting information and perception is interfered with. Similarly, Triesman (1962) has suggested that rivalry may reflect the competition between 'corresponding fibres' for individual common pathways, and tentatively identifies these common pathways as binocularly driven cells in visual cortex. Jung (1961) and Bishop (1971) have also assigned a major role in the explanation of rivalry to the inhibitory convergence of monocular inputs at the striate cortex.

Since, according to this classical fusion theory, the cross-correlation or matching of the two inputs is undertaken on a point-to-point basis long before there is an analysis of the more complex features of the stimuli, nothing more than a primitive analysis of the suppressed stimulus is assumed possible. If correct, then this aspect of the classical fusion theory of stereopsis would contradict the thesis that a rather sophisticated analysis may be afforded the suppressed stimulus.

There are logical objections to the notion that a 'point analysis' of each monocular field is an adquate basis for a comparison or cross-correlation of the two fields. Since a stereogram of any level of complexity involves any number of 'points' one must ask what determines which contralateral pairs of points will link up to provide information as to disparity. Indeed, why doesn't a point in one field associate itself with any number of points in the contralateral field to yield a large number of phantom objects at varying depth? (cf Julesz, 1971).

Implicit in much of the earlier work, then, is the notion that the object-points must be on similar forms or contours in order to be matched. Clearly, however, this demands that the

analysis of each field should proceed to a level where such forms or contours are discriminated.

In addition to these logical objections, Kaufman (1964b, 1967) has provided a number of stereograms which, though capable of yielding the impression of depth, involve presenting different forms or contours to the two eyes. Thus, the letters "asdqwadwadwadpoiuy" may be presented to one eye and the letters "asdpsnpsnpsnqpoiuy" to the other, and an impression of depth will result. Kaufman concludes, therefore, that 'any perceptible patterning can yield depth perception provided that the patterning is disparately represented in the two eyes'(1967). Similarly, Ramachandran et al (1973a, b) and Harris and Gregory (1973) have also demonstrated that the disparity information that yields stereopsis may involve very abstract features of the two monocular fields. We may, therefore, reject this second aspect of the classical theory of depth perception, which discourages the notion that suppressed information is subjected to anything other than a primitive analysis.

2.1.6 Peripheral factors contributing to rivalry

Though all of this, and what follows, is to emphasize the central nature of rivalry, it is not to be denied that peripheral factors may make some contribution. Thus, Kaufman (1963) has demonstrated that the extent of the spread of suppression from a contour is, to a large extent, correlated with the existence of nonconjugate eye movements. There is no suggestion, however, that such movements are the cause of the suppression. Similarly though the data here is a little inconsistent, changes in the pupillary response mechanism have been associated with rivalry alternations. Lowe and Ogle (1966) discovered that when the rivalling fields had different overall luminosity, a small pupillary constriction was found to occur whenever the dominant image changed from the dimmer to the brighter stimulus. The magnitude of this pupillary constriction generally increased with increases in the difference between the two luminosities. More recently, Richards (1966) and Bokander (1967) have confirmed earlier observations (Barany and Hallden, 1948; Harms, 1937; Wirth, 1952) that there exists a differential in the extent of pupillary constriction depending whether a light stimulus is presented to the currently dominant or suppressed field. As with the possible contribution of nonconjugate eye movements, so with pupil responses, it must be said that these can not explain the suppression itself. Firstly, the change in the state of the pupil that correlates with dominance is relatively small and certainly not responsible for the complete phenomenal suppression (indeed, in the studies of Barany and Hallden, and Lowe and Ogle, subjects were always aware of the light stimulus which initiated the pupil constriction, even in the suppressed condition). Secondly, as with accommodation, the two eyes behave in unison and so it is difficult to conceive of the pupillary mechanism being capable of favoring one of the monocular fields in the voluntary control of rivalry.

2.2 Direct Evidence that the Suppressed Stimulus in Rivalry is Encoded

2.2.1 Introduction

With the content of the preceding sections providing the context for a more selective review of the literature, it may be asked whether there exists any more direct evidence that the suppressed stimulus in rivalry nevertheless undergoes a continuous analysis. In considering this evidence it will be useful to treat separately data relating to the analysis of the structural content and data relating to the analysis of the meaningful content of a stimulus.

2.2.2 Analysis of structural content

Experiments suggesting that a structural analysis is undertaken on currently suppressed stimuli:

Levelt's (1966) thesis relates changes in the 'stimulus strength' of a rivalling field to subsequent changes in the temporal course of the phenomenon. His review of a large number of studies suggested that "the mean duration of the dominance of the stimulus in one eye is independent of the strength of this stimulus; the duration is assumed to be dependent only upon the strength of the stimulus in the contralateral eye" (Levelt, 1966, p 225). His own experiments provided direct support for this. Thus, increasing the stimulus strength of a rivalling field, by increasing the contrast or bringing it into sharper focus, served to reduce the time for which that field remained suppressed but did not change the time for which it remained dominant. Fox and Rasche (1969) have since confirmed this in a direct test. A literal interpretation of this thesis suggests then, that at any instant the probability that a shift in dominance will occur is dependent upon the properties of the currently non-dominant stimulus as they are revealed by a current analysis of the sensory information. Confirmation of this interpretation would, therefore, provide evidence that the structural details of a

suppressed stimulus are discriminated.

Unfortunately, Levelt's data does not provide this confirmation. His procedure did not eliminate the possibility that the mechanism responsible for the rivalry alternations responded to the properties of the currently non-dominant field by referring to some stored representation (made available during a preceding dominance phase of the field) rather than to the results of a current analysis of the sensory information. It is in this sense that Levelt's experiments fail to offer 'proof' that the structural content of the suppressed field is analysed.

The studies of Ramachandran et al (1973) and Kaufman (1964a,b), in demonstrating that rather complex features of visual stimuli may carry the disparity information which yields the impression of depth, suggest, as has already been argued, that both fields are fully analysed before the matching process, that is the basis of stereopsis, occurs. Similarly, we have seen that successful attempts have been made to devise stereograms which, though involving the suppression of a monocular field, nevertheless yield the impression of depth whilst this suppression occurs (Asher, 1953; Julesz, 1961, 1971; Kaufman, 1964a,b; Ramachandran et al, 1973; Ogle and Wakefield, 1967). However, the same limitations that Levelt's studies suffer may in general apply to these demonstrations, viz. that the suppressed information may contribute to the phenomenon via a stored representation of itself rather than directly as a result of a current analysis. This is particularly possible in view of the fact that with such stereograms the impression of depth requires time to emerge. Within this time it is likely that each field will have attained a state of dominance and found some form of internal representation. Two of these stereoscopic demonstrations, however, are not subject to this criticism. Thus, Kaufman (1964b) devised a stereogram with which he discovered that not only did one field suppress the other, but it did so immediately and continuously upon presentation. Though one of the fields failed to attain a

state of dominance at all, the impression of depth emerged. Likewise, Julesz (1961) has shown that when one member of a stereopair is apparently blurred, the perceived image is stable and corresponds to the sharper member of the pair. Nevertheless, depth perception is still obtained.

The studies reviewed in this section go some way, therefore, towards providing proof that the structural information within a stimulus continues to be analysed during its suppressed phases.

2.2.3 Analysis of meaningful content

The following group of studies demonstrate that the resolution of a conflicting situation that arises when two different monocular stimuli are presented dichoptically, may not be attributed solely to the formal properties of the two stimuli. Rather, in these experiments, the meaningful content of the two stimuli is found to play an important part in determining this resolution. These studies may be taken further however.

The general paradigm involves presenting two stimuli dichoptically and asking subjects to report their perceptual experience. From these reports it is inferred which of the two stimuli was dominant, and the basis for the preference. Clearly, depending how strict is the definition of dominance, this paradigm is capable of providing evidence that is relevant to the present thesis. Thus, if a stimulus is only classified as the dominant one if it is the only stimulus to be perceived, or is the first stimulus to be perceived, then it would be justifiable to conclude that the meaning of the stimulus going unperceived was nevertheless discriminated: how else could a meaningful resolution be effected? For example, if two words are paired in a stereoscope, with one having more emotional connotations than the other, and subjects report only the emotional, we may conclude that the meaning of the unseen word was nevertheless discriminated: how else could the more emotional of the two stimuli be selected? Rommetveit et al (1969) make the same point when remarking that

"choice of the alternative which fits the context, presupposes that both alternatives were available to the perceiver at some level and some stage of processing" (p 263). If these studies are to have a bearing on the present thesis, therefore, it is important that this rather strict definition of dominance be adopted. If a much weaker definition of dominance is accepted, such as that stimulus which, though alternating in dominance with the other stimulus, is dominant for a greater proportion of time, or in general is seen more clearly than the other, then it is not justifiable to conclude that the meaning of a currently unseen stimulus is analysed, for the same reasons that Levelt's data did not allow the literal interpretation of his thesis.

The first group of studies concerned with meaningful resolution suffer this inadequacy of not employing a sufficiently strict definition of dominance. Thus, dominance is defined either as (i) the stimulus seen to the total exclusion of the other, (ii) the stimulus seen first, or (iii) the stimulus dominating for the greater proportion of time. The acceptance of dominance reports of the last category is unfortunate. However, a number of studies, though failing to make the important distinction between the first two and the last category, have employed a sufficiently brief exposure duration for the incidence of rivalry alternations to be unlikely. Thus, Bokander (1969) and others have reported that exposures of approximately one second are too short for more than a single percept to emerge. Studies involving such brief presentations therefore provide slightly stronger support for the hypothesis that the meaning of the unseen alternative is nevertheless encoded.

Because the studies to be discussed in this section were undertaken with hypotheses in mind that are a little different from that under consideration, they suffer some additional shortcomings. First, in some instances few experimental details may be given, including the exposure duration. Second, invariably

the experimenters have relied on subjects' descriptions of what they saw in order to determine whether one or two stimuli were seen and which of these dominated. An alternative explanation for some of the results, particularly where emotional material is involved, is therefore one based on 'response' factors.

Finally, before discussing this and the following group of studies, it must be stated that in demonstrating the continued discrimination of the 'meaning' of suppressed information, these studies add to those of the preceding section, since it must be assumed that the structural analysis of a stimulus precedes the determination of its meaning.

Experiments which suggest that an analysis for meaning is undertaken on currently suppressed information:

Kausfer and Riess (1960), in arguing the case for employing binocular rivalry in psychotherapeutic research, report a pilot experiment that involved presenting male and female nude pin-ups, or symbolically-related stimuli, separately to the two eyes. They report that the stimulus which emerged as the dominant one was dependent upon the sex of the observer. Thus, for their male subjects, a male pin-up and a picture of the Washington monument (when paired with the Jefferson memorial) predominated. For their female subjects, the opposite held true. Unfortunately the authors do not report the details of their study, including the exposure duration, or the type of analysis employed. They do, however, report that their male and female subjects in general saw <u>first</u> the stimulus that overall predominated, and this suggests that the same results would have emerged had a stricter definition of dominance been employed.

Kohn (1960) paired emotional and neutral words in a stereoscope and discovered that subjects who had emotionally-toned fantasy themes in response to the TAT, and who also reported themselves to be relatively more hostile, tended to see the emotional word. Unfortunately Kohn does not report the exposure

duration involved, and defines the dominant word as the word first seen or the word predominantly seen. Again, however, subjects reported that the word first seen tended to be predominant.

Wells and Bell (1962) presented three groups of subjects, classified as over-achievers, under-achievers or equal-achievers, with six exposures of authority, peer group and neutral figures in a dichoptic situation. The authors found that the peer figure was recognised more frequently by the over-achievers than by the equal-achievers, and that the authority and neutral figures were recognised less frequently by the former group. There were found to be no corresponding differences between the equal and under-achievers. Though the brief exposure (0.5 sec) would be expected to preclude the possibility of subjects experiencing rivalry alternations (Bokander, 1969), the authors reported that subjects did occasionally see and recognise two figures, and their analysis was not confined to those trials in which subjects only decided one figure. However, it would seem likely from the data they report, that the above finding would still hold if the analysis were confined to those instances in which only one figure was described. One further weakness of the study was that the experimenters could only infer, on the basis of subjects' correct descriptions of the figures, whether one or two figures were seen. They did not ask subjects to report this fact directly.

Reitz and Jackson (1964) associated different nonsense syllables with a variety of pictures that had previously been scaled with regard to pleasantness. When syllables that had been associated with pleasant and unpleasant pictures were paired and presented dichoptically in the stereoscope, the relatively more unpleasant syllable was seen more often by subjects scoring in the shallow-effect direction on a personality scale. Though the authors could distinguish from subjects' responses whether one or more than one syllable had been perceived, this distinction was not maintained in the analysis. As did Wells and Bell, these

authors also relied on subjects' descriptions of what they saw in order to infer which stimulus had dominated.

Reynolds and Toch (1965) studied the "Engel Effect". To produce this, two different portraits were presented dichoptically, with initially just one portrait illuminated. Gradually the dark portrait was brightened in small steps until the two fields were equally bright. Then the brightness of the initially-illuminated portrait was gradually reduced. The Engel Effect consists of the fact that no phenomenal change may be reported at any stage in this sequence, despite the fact that the observer ends by seeing a different face. Ittelson and Seidenberg (1962) made the point that, the more dissimilar the two portraits are, the more likely the transition is to be noticed, and Reynolds and Toch tested the hypothesis that the point (threshold) at which subjects noticed the transition, from Negro to Caucasian and vice versa, would depend upon whether the observer was racially prejudiced. Non-significant trends in their data did suggest that prejudiced subjects report the transition from Negro-Caucasian, and vice versa, at a later stage than non-prejudiced subjects, and that for the former subjects the transition from perceiving one face to the other is more abrupt and less likely to involve a period in which the two faces are fused in some way. These trends suggest then, that subjects were capable of discriminating the nature of the originally dimly illuminated figure before it actually contributed to perceptual experience. Unfortunately, Beloff and Coupar (1968) undertook a similar experiment and, though their results are a little inconsistent, reported the opposite finding, viz. that subjects having a negative attitude towards coloured people report the transition (black-white or white-black) <u>earlier</u> than subjects with a positive attitude.

Bagby (1975) observed that the cultural characteristics of the conflicting visual presentations are differentially perceived by members of different societies. Thus, subjects more readily perceived the picture whose content was drawn from

their own culture than an equivalent picture relating to a different culture when these were presented dichoptically. Whilst Bagby employed an exposure duration of 60 seconds, data gathered only during the first 15 seconds was analysed. His definition of dominance was relatively strict in that it incorporated reports of seeing only one slide throughout and the slide seen first. Unfortunately, however, his definition also incorporated reports of a picture appearing to be present most of the time.

Van de Castle (1960) presented, simultaneously and for one second, aggressive and neutral words (in all combinations) in a stereoscope. He discovered that sensitisers (defined as those subjects scoring above average on the Welsh Anxiety Scale and below average on the Welsh Repression Scale) as compared to defenders, reported more aggressive words and few nonsense words (composites, formed from a combination of the letters from the two words) to be dominant when the stimulus pair contained an aggressive word. Unfortunately, in his analysis Van de Castle did not distinguish occasions on which only a single word was perceived and occasions on which both were seen though one dominated. He does point out, however, that only one word was seen on over two-thirds of the trials.

Green and Money (1962) presented two pictures containing human figures, one of each sex, against backgrounds of similar shape and shading and, though many of the comparisons were insignificant they did find that men were more likely to report the female picture as dominant. Again, however, a relatively long exposure was employed (ten seconds), sufficient for alternations to occur, and Green and Money's definition of dominance included instances of where both pictures were seen, one more clearly than the other.

Lo Scuito and Hartley (1963) presented ten Jewish and ten Catholic subjects with pairs of symbols, words or pictures (one Jewish and one Catholic) dichoptically, and observed a significant tendency for subjects to report seeing material

related to their own culture. Moreover there was a significant correlation between the tendency to report seeing material from the other culture, and a measure of subjects' open-mindedness. However, though the verbal material was presented for only one second on each trial, the pictorial material was presented for a relatively lengthy period (30 seconds) which would presumably have allowed alternations in dominance to occur. In addition, though the authors could distinguish those occasions on which only one stimulus was perceived, this distinction was not observed in the analysis.

Finally, concluding this section, Ono, Hastorf and Osgood (1966) had a sample of portrait photographs rated on a number of semantic differential scales. When these portraits were subsequently paired and presented dichoptically in a stereoscope, the occurrence of rivalry was found to be dependent upon there being a degree of incongruity between the two portraits. Incongruity was defined as the occupation of opposite positions on at least one semantic dimension. Thus, for any specific combination of two portraits, a greater proportion of observers experienced fusion among those who assigned a similar semantic profile to the two stimuli. The authors defined a fusion response, the alternative to rivalry, as a report of seeing just one face throughout. The fusion category incorporated instances where a monocular stimulus dominated completely and instances where a composite of the two monocular faces was perceived. If the same conclusion could still be drawn on the basis of an analysis that was confined to the first category of fusion-response, then there would be support for the hypothesis that the character of the unseen or suppressed face is nevertheless discriminated: how else could the two faces have been discovered to be incongruous? Since no distinction was made between the two types of fusion-response, this conclusion can not be drawn. The reason is that in the case of fusion that involves a composite of the two faces, it is possible that the different features contributing to the composite were themselves incongruous, and as a result encouraged the search for more congruous alternatives - hence the fluctuation. Thus,

incongruity in this instance could have had its effect on the resolution of the conflict via the perceived image itself and not via the suppressed information.

To summarize, though each of the studies reviewed in this section suffers one or more shortcomings, collectively they strongly suggest that the meaningful content of a suppressed stimulus may be discriminated.

Experiments which offer more direct evidence that the meaningful content of a suppressed stimulus is discriminated:

Hastorf and Myro (1959) studied another of Engel's observations. Engel (1956) presented two portraits dichoptically for one minute, one of which was inverted. Though subjects often were aware of both portraits, it was discovered that the upright face was seen more often, more clearly, and more completely than the inverted face. The relatively long exposure duration used, however, allows for the possibility that the right-side-up portrait was reported to predominate over the confusing upside-down one, even though they were seen equally well. In other words, the results could have reflected a response bias. However, despite avoiding such alternative interpretations by sufficiently reducing the exposure duration to ensure that only a single percept was reported (0.1 and 0.2 seconds), Hastorf and Myro (1959) were able to confirm Engel's observations.

Galton (1907), Engel (1958) and Drever (1957) observed that when two different faces were presented dichoptically and a single composite face was perceived, this face was always considered by the subject as more attractive or satisfactory than either of the composite faces. These authors demonstrated, therefore, that the attractiveness of a face, or of certain of its features, may be discriminated despite the suppression of the whole face, or these features: how else could a more attractive face or the most attractive instance of a feature be selected?

In a similar study, Beloff and Beloff (1959) went a little further and presented each subject with his own photograph as one of the two faces that were viewed dichoptically. In this instance, even though subjects were unaware that their own portrait was involved, the composite appeared to be even more attractive. It appeared to these authors, therefore, that subjects were able to recognize their own face despite the fact that it suffered suppression to the extent that recognition was impossible, and they concluded that "somewhere in the visual cortex a complete projection of the self photograph must exist ...." (p 277).

Toch and Schulte (1961) presented tachistoscopically (0.5 seconds) a violent and neutral picture dichoptically, to subjects who had completed a course in law enforcement, and to control subjects who had not. Compared to the control subjects it was found that policemen perceived the violent rather than the neutral picture. The authors comment that the exposure duration used ensured that subjects quite clearly perceived only a single picture, which almost always corresponded to one of the monocular fields.

Shelley and Toch (1962) presented dichoptically, and tachistoscopically (0.5 sec duration), a picture that represented some form of anti-social behaviour (e.g rape or murder) with a picture that was more neutral in this respect, though very similar in structural content. The brief exposure, together with the choice of picture-pairs that were mutually exclusive in the sense that they were incapable of fusing into a single percept, ensured that subjects saw only one of the two pictures. Employing institutionalised offenders as subjects, it was discovered that those who revealed a tendency to perceive the anti-social alternative were more likely to engage in anti-social conduct within the institution. In a similar study, Berg and Toch (1966) presented pictures that represented some form of impulsive behaviour, and control pictures, tachistoscopically and dichoptically. The authors discovered that those inmates

who had a tendency to act impulsively were more likely to perceive the impulsive pictures rather than their controls.

Moore (1966) presented male and female subjects with violent and non-violent pictures dichoptically. The short exposure duration of 0.5 sec ensured that just a single percept resulted and Moore found that males perceived significantly more violence than females. As a check that this did not reflect an unwillingness on the part of the female subjects to report aggressive material, the author included 'lie' stereograms in the experiment, which consisted of two different pictures each having violent content.

Davis (1959) used verbal material. For approximately one second he presented two different words dichoptically and discovered that when the two words differed in frequency of usage, the more frequent of the two was reported most often. In addition, when one of the words was more emotional than the other (being associated with a response latency of at least 2.5 seconds in a word-association test), this word was reported significantly less frequently than the other.

Finally, a series of experiments by Rommetveit provide perhaps the best and most intriguing evidence that the resolution of a rivalrous situation may be meaningful and, therefore, that the content of the two monocular fields is fully appreciated despite the suppression of one of them.

Rommetveit, Toch and Svendsen (1968a) presented dichoptically, for either 170 or 370 msec, two very similarly-structured words (hell and tell) following (by 3-4 seconds delay) or simultaneously with an additional word, which was presented to both eyes and which provided either a contrasting context (e.g heaven) or a contingency context (e.g devil) with respect to one of these two words. The authors found that the induction of the context was a powerful determinant of which of the two words was perceived. With the contrasting context

the word whose meaning was the opposite of the context word (i.e hell) was perceived most often, whilst with the contingency context the word having the same area of reference as the context word was perceived. There was, however, a significant interaction with mode of presentation, such that the former context was most influential when the context and test words were presented simultaneously and vice versa. In general then, subjects most often perceived the stimulus whose meaning had been made most salient by a context word.

In a second study, these same authors (1968b) demonstrated the effects of other types of context. The different contexts considered were 'meaningful' (sweet wine vs sweet your), 'grammatical' (wrinkled wine vs wrinkled your) and associated (beer wine vs beer your). When these sequences of two words were presented dichoptically, for 370 msec, the context provided by the first word (which was common to both eyes) determined which of the two alternatives for the second word was actually perceived. In these three examples, then, wine tended to dominate.

In a slightly different, third study, Rommetveit, Berkley and Brogger (1969) demonstrated just how late in the 'perceptual process' is the selection of a percept in rivalry. These authors demonstrated that if presented with stereograms of the following kind, SHAR/SHAP, SOR MIK/SUR MIL, subjects will perceive a meaningful stimulus (i.e SHARP, SOUR MILK). Indeed, under some conditions subjects reported that the word SAINT appeared equally clear perceptually, whether it arose as a result of the subject being presented with SANT/SINT or SAINT/SAINT dichoptically. Perhaps most dramatically, these authors discovered that subjects perceived the word FRIEND when presented dichoptically with the two letter sequences FCIAND and FREUMD. This latter study complements the former studies and provides support for the hypothesis that information that fails to contribute to perceptual experience is nevertheless subject to a thorough analysis. Thus, in order to make FARM

and not FRM, FAM or FRAM out of FAM/FRM, both the A and R must register before the percept is generated.

In summary, it is contended that this last group of studies are not open to the same criticism as the studies of the preceding section, and offer much more convincing evidence that the meaningful content of a suppressed stimulus may be discriminated.

2.3 Negative Evidence

Before leaving the literature, consideration must be given to a number of studies which appear to favour an explanation of rivalry that involves relatively simple, peripheral mechanism whereby rivalry is treated as a rather passive competition between the two monocular images.

Fox and Check (1966a) superimposed a spot of light, tachistoscopically, on one of the two rivalling fields, and subjects were asked to respond as quickly as possible when this test flash was observed. The authors arranged that this flash could occur whilst the field upon which it was superimposed was either dominant or suppressed. They observed that the reaction time was longer in the latter case. In a similar study, Fox and Check (1968) employed the movement of a small stimulus rather than a spot of light and, as before, observed that subjects' reaction times were longer when this stimulus was superimposed on a monocular field whilst it was suppressed. In another study, Fox and Check (1966b) introduced, tachistoscopically, various letters into a rivalling field, during either its dominant or suppressed phases, and discovered that more letters were correctly recognized in the former condition. Finally, Wales and Fox (1970) used a spatial, two-alternative, forced choice task, in which a light flash appeared in either the upper or lower half of a rivalling field. The authors observed that detection performance was significantly worse when the test flash was presented whilst the field upon which it was superimposed was suppressed.

Fox and colleagues concluded from these studies that rivalry suppression reflects an inhibitory process that effectively reduces subjects' sensitivity to information in a monocular channel. Since, in each case, the test stimulus was different from the rivalling stimuli, it was also concluded that this process was a non-selective, blanket inhibition of

all information in a monocular channel. The hypothesis that rivalry was essentially a mutual competition between the two monocular channels was made more explicit in a further paper (Fox and Rasche, 1969). There are a number of problems with this interpretation of the data. First, a lengthened reaction time may reflect not the increased time necessary for a weakened signal to be recognized, but rather the time needed to shift attention from one channel to another. Indeed, the lowered recognition performance, when stimuli are presented in a currently suppressed field, may reflect this insofar as the presence of a minimum time to switch channels may mean that by the time the relevant channel is being sampled, the trace of the test stimulus is weakened. It may be noted that Swets and Kristoffersen (1970) have offered a similar interpretation of the reduction of d' when signals are presented in a non-attended ear in dichotic listening. Second, the decreased sensitivity which accompanies suppression in these studies, is very modest when compared to the phenomenal effects of rivalry (cf Wales and Fox, 1970). It would appear unlikely, therefore, that this decreased sensitivity could explain the phenomenal suppression. Third, as we have seen, there is much evidence to suggest that rivalry need not simply be a competition between the two eyes, rather the different aspects of the two monocular stimuli may rival independently of each other.

2.4 Summary of Literature Review

The existing literature does not contradict the thesis that is to be developed. The existing approaches towards rivalry that conflict with the notion that it is a central phenomenon, are seen to be themselves at odds with the evidence. Moreover, those studies which have a more direct bearing on the hypothesis, though not designed with this in mind, do not lead us to reject the notion that suppressed information is fully analysed.

The fact that subjects may voluntarily control the course of rivalry not only implicates rather central processes in the phenomenon but, for Helmholtz at least, offers proof that the monocular fields remain independent, with the information in each being fully analysed regardless of the state of dominance. The fact that peripheral factors, such as changing accommodation, do not mediate this voluntary control is consistent with this conclusion.

Encouraged by the compactness and relative independence of the two monocular channels are the alternative explanations of rivalry based on the concepts of reciprocal inhibition and adaptation. It was argued, however, that such processes do not contribute significantly to the appearance of binocular rivalry. Thus, for example, successive dominance phase durations are found to be independent. Moreover, the notion that rivalry reflects a competition between the two monocular channels, each acting in a unitary fashion, was questioned on the basis that the different parameters of the two rivalling stimuli may rival independently of one another.

Implied in the traditional fusion theory of stereopsis is the belief that suppressed information can not contribute to perception to yield the impression of depth. However, evidence was presented, which included successful attempts to produce the impression of depth from retinal disparity despite

the suppression of a monocular field, that militates against such a theory of stereopsis. Moreover, an additional aspect of the fusion theory of stereopsis which implies that only a primitive analysis of the suppressed stimulus is undertaken, viz. the notion that the two images are fused (or not) on the basis of a point-to-point matching process, was also seriously questioned. It was seen, for example, that quite abstract features of the monocular stimuli may carry the disparity information.

A review of the experiments that bear directly on the problem of the analysis of suppressed information, revealed support for the notion that this analysis is sophisticated - sufficiently so to mediate a response to meaning. To draw such a conclusion it was argued that, under conditions where only a single stimulus is perceived, the meaningful resolution of two competing stimuli implies that the meaning of both was available, albeit at an unconscious level.

Finally, it was pointed out that there were alternative interpretations of the 'negative' evidence provided by Fox and his colleagues. Indeed, these alternative interpretations accord with the theoretical analysis that is developed later.

Against the context provided by these studies, two experiments were undertaken. These experiments involved the presentation of additional information to one of two rivalling fields, during either its suppressed or dominant phases. By demonstrating that the course of rivalry is sensitive to this information in the former condition, it was confirmed that suppressed information is fully analyzed. Since in the first experiment the paradigm itself was under test, the additional information involved a fundamental parameter, viz. movement.

CHAPTER 3 EXPERIMENTAL CONFIRMATION OF THE HYPOTHESIS CONCERNING THE FATE OF SUPPRESSED INFORMATION IN BINOCULAR RIVALRY

Two experiments are reported which focus on the fate of the information residing in a suppressed eye during binocular rivalry. It is demonstrated that the temporal course of rivalry is sensitive to the movement (Experiment 1) and to the meaning (Experiment 3) of a subliminal stimulus within the currently suppressed field. The effects are seen to confirm a literal interpretation of Levelt's (1966) thesis which relates changes in the 'stimulus strength' of a rivalling field to subsequent changes in the temporal course of the phenomenon. This interpretation is consistent with the hypothesis that, despite phenomenal suppression, a full analysis is undertaken on the currently non-dominant stimulus. An additional experiment (Experiment 2) confirms that the movement of a subliminal stimulus may be discriminated, by demonstrating that the course of autokinesis is sensitive to the presence of such a stimulus. The data are related to the notion that there are parallel visual systems, and it is argued that the second visual system (superior colliculus-temporal cortex) is responsible for the visual system's sensitivity to the non-dominant stimulus.

3.1 EXPERIMENT 1 THE SUBLIMINAL PERCEPTION OF MOVEMENT AND SUPPRESSION IN BINOCULAR RIVALRY

In the first experiment an attempt was made to determine whether the perceptual system is capable of discriminating a moving pattern that is presented within the currently non-dominant field in binocular rivalry. More specifically, it was asked whether the introduction of movement into such a field would reduce the amount of time for which it remained non-dominant. Reference to Levelt's (1966) thesis, which relates changes in the 'stimulus strength' of a rivalling field to subsequent changes in the temporal course of the phenomenon, provided more precise predictions. Consistent with his preliminary definition of 'stimulus strength', it was assumed that adding movement to a field would serve to increase that field's strength.

Quite apart from its relevance in this respect, Levelt's thesis has a direct bearing on the experimental problem since his central proposition is that 'the mean duration of the dominance of the stimulus in one eye is independent of the strength of this stimulus; the duration is assumed to be dependent only upon the strength of the stimulus in the contralateral eye' (Levelt, 1966, p 225). It has been argued already that a literal interpretation of this suggests that at any instant the probability that a shift in dominance will occur is dependent upon the properties of the currently non-dominant stimulus as they are revealed by a current analysis of the sensory information.

Unfortunately, Levelt's data do not provide this confirmation. His procedure did not eliminate the possibility that the mechanism responsible for the rivalry alternations responded to the properties of the currently non-dominant field by referring to some stored representation (made available during a preceding dominant phase of the field) rather than to the results of a current analysis of the sensory

information. This problem was circumvented in the present study by having the introduction of movement to a rivalling field restricted to coincide with either its non-dominant or dominant phases.

Finally, it was reasoned that whatever aspect of the visual system is capable of responding to information in the non-dominant field, it is a likely mediator of subliminal perception (cf Dixon, 1971) since ipso facto it can function in the absence of a perceptual (phenomenal) adjunct to the information with which it is dealing. As a test of this, a condition involving the movement of a subliminal stimulus was incorporated in the experiment.

Method

Each subject reported the alternations between rivalling red and green fields that were presented to his right and left eyes respectively (cf Fig 2, 3). Preliminary experiments demonstrated that providing a difference in overall size of the fields (the red being smaller than the green) served to discourage (i) the two fields from fusing to yield 'cortical yellow', and (ii) the occurrence of a piecemeal form of rivalry in which different, localized parts of the fields behaved independently.

Variation of the stimulus conditions involved changes to the red field. The six trials undertaken by each subject were segregated into two blocks of three, according to whether the stimuli that were superimposed on this field were at a supraliminal or subliminal (as defined below) level. In addition to a trial involving the presentation of a moving pattern (movement condition), each block incorporated a control trial during which the same pattern remained stationary (stationary condition), and a further trial during which no additional stimuli were presented to the red field (blank condition). With the stationary trial always being given between the blank

Figure 2

(a) The rivalling stimuli employed in the experiment. G, the homogeneous green field that was presented to subject's left eye. R, the red field that was presented to the contralateral eye: a sample of the pattern that was projected on to this field being illustrated. Note that upon projection only the lighter parts of this pattern would be visibly superimposed upon the otherwise illuminated, homogeneous red field. In this sense the figure is unrepresentative of the conditions that pertained to the experiment.
(b) The relative positioning of the two fields when seen through the stereoscope. The red field is represented as dominant. The difference in size of the two fields provided a green 'rim' which tended not to be suppressed by the red field.

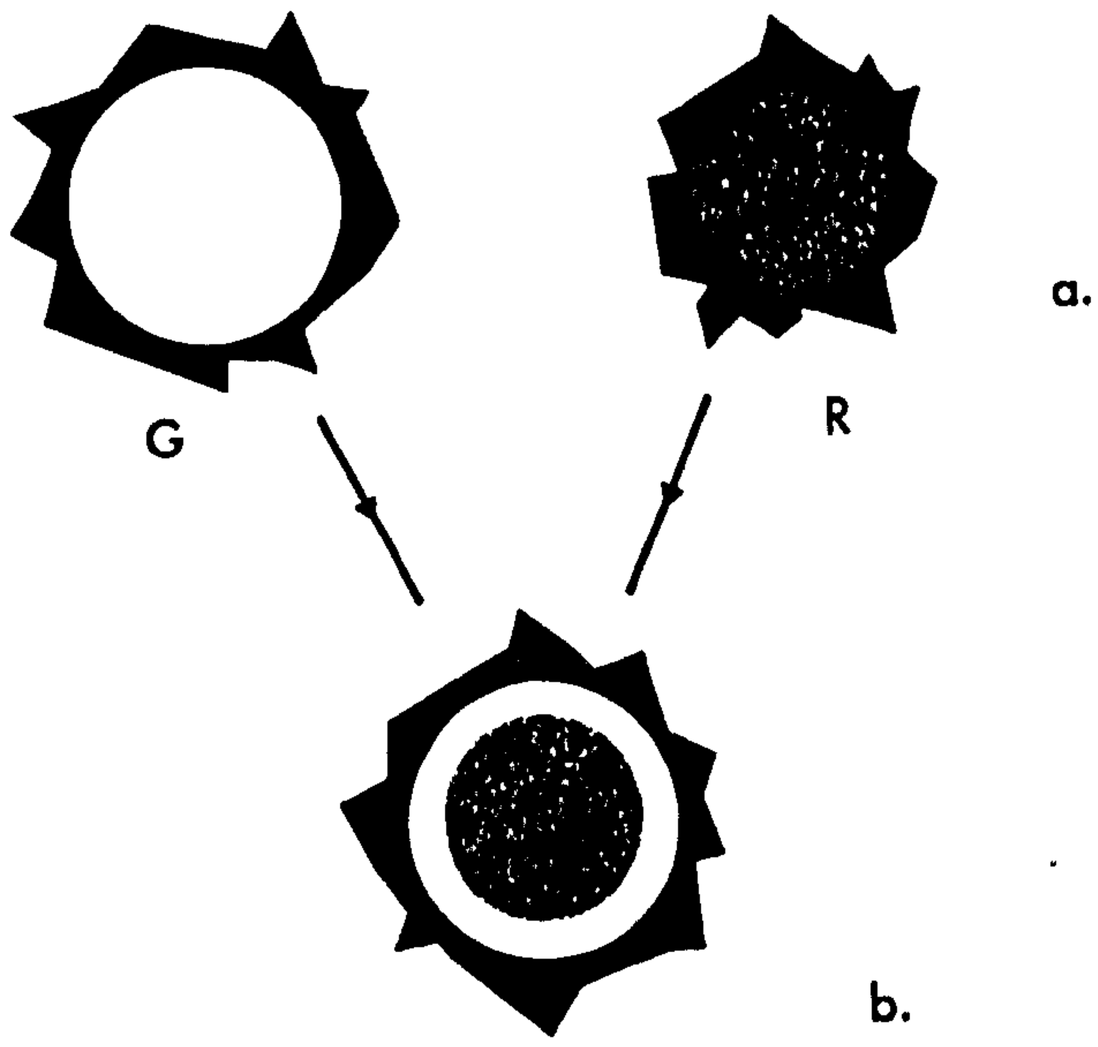
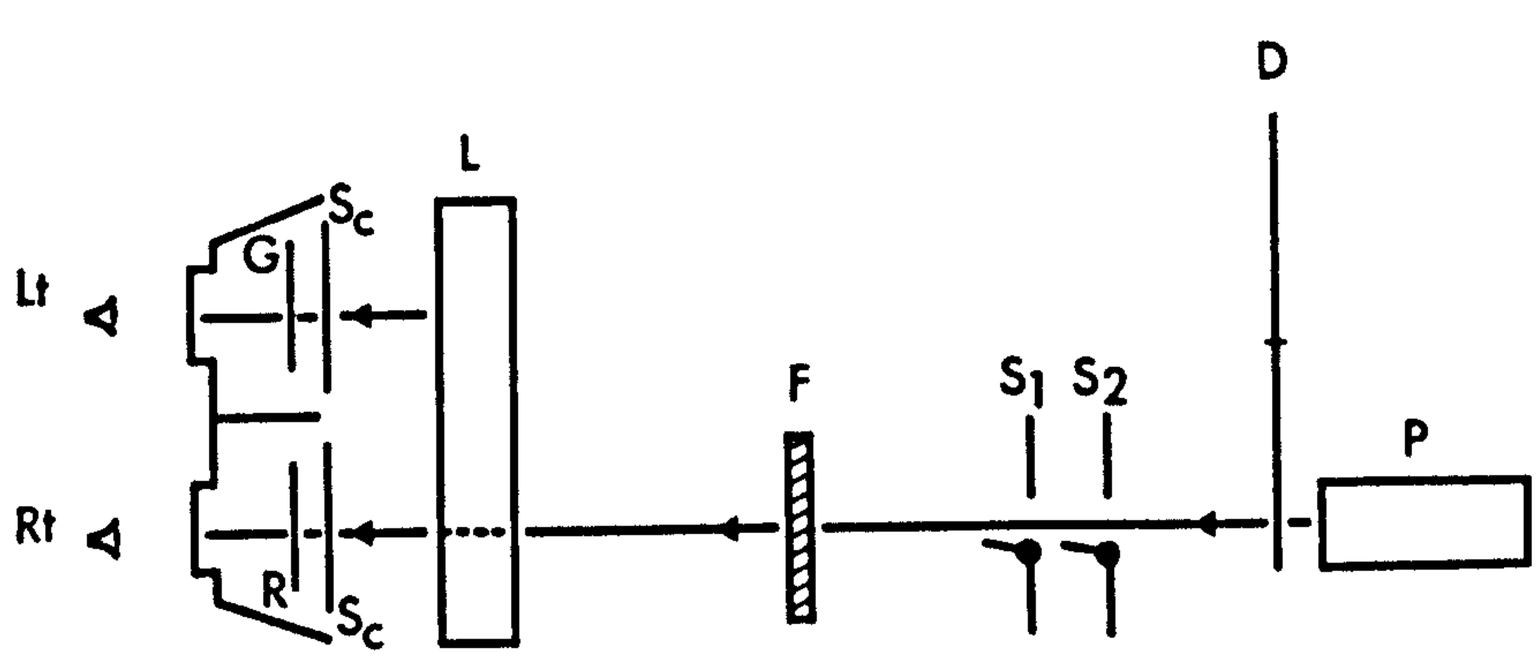

G
R
a.
b.

Figure 3

Schematic diagram of the apparatus. P, projector; D, rotating transparent disc bearing the pattern illustrated in Fig. 2; S_1 and S_2, shutters; F, neutral density filter; L, flourescent lamp positioned behind and above the stereoscope; Sc, screens placed in the fields of the stereoscope; G and R, the green and red filters; Lt and Rt, subject's left and right eyes.


D
L
Sc
G
Lt
F
S1
S2
P
Rt
R
Sc

and movement trials within any block, and half the subjects undertaking the sublimal condition first, there were four different arrangements for the trials. An equal number of subjects undertook the trials in each of these orders.*

When the pattern was superimposed on the red field, its presentation was made contingent upon the field reported to be currently dominant. For one group of subjects its presentation was restricted to coincide with the dominant phases of the red field (dominant condition); whilst for a second (independent) group, its presentation coincided with this field's non-dominant phases. Independent groups were employed in this way in order to avoid (i) fatiguing subjects, and (ii) the transfer effects that were evident in some preliminary observations employing the same paradigm.

From the data recorded on each trial the number of alternations (changes in dominance from one field to the other) and the average duration of dominance of each field (mean dominance time) could be calculated.

Apparatus

Semi-transparent tracing-film screens were placed in each field of a modified Unis-France stereoscope. Between these and in the right and left eyepieces were placed, respectively, red (Ilford:205) and green (Ilford: 625) colour filters. Whilst the former transmits freely in the 6400A to infra-red range (with heavy absorption at other wavelengths) the latter is restricted to between 5100 and 5900A. Transilluminated by a small fluorescent lamp (Opal Striplite - 30V 30W 221mm) positioned behind and above the stereoscope, the differently coloured stereoscope fields served as the rivalling images. The red and green fields subtended $11^{\circ}18'$ and $15^{\circ}38'$ respectively, and ignoring the small changes that were made in order to counterbalance eye dominance, their luminance measured 1.5 log ft lamberts.

* time limitations precluded a symmetrical design that would have allowed the importance of eye/colour and movement/colour combinations

The moving pattern was projected on to the red field by passing the edge of a rotating transparent disc through the focal plane of a projector (Aldis Tutor 1000; lamp, Philips M9, 240V, 300W, A1/178). Commercial Letratone, pattern LT 100 (a quasi-random pattern, cf Fig 2), was applied to the disc. When viewed through the stereoscope, this pattern traversed a linear path, in an upward direction, with a velocity of 20deg. $sec.^{-1}$ The irregular and fine texture of the pattern ensured that no fluctuation in gross intensity of the red field was confounded with the movement. For the stationary trials the transparent disc was prevented from rotating, whilst for the blank trials, a shutter, placed immediately in front of the projector, was closed.

For the independent control of the gross intensities of the two fields crossed polaroid filters were mounted in front of each eyepiece. Positioned between projector and stereoscope was one of a series of Kodak Wratten neutral density filters. The critical effect of interposing a filter in this way was to decrease the contrast between the pattern and the ground upon which it was projected.

Two microswitches were provided for the subject to report the rivalry alternations. With one switch connected to a camera shutter mounted in front of the projector, the presentation of the pattern could be restricted to the dominant or non-dominant phases of the red field. In addition, each switch was connected to an electronic timer, and an even counter, and to one channel of an Esterline Angus multiple channel pen-recorder.

Subjects

Forty-four subjects took part in the experiment. All were undergraduate students at University College of London, though none were students of psychology.

Procedure

The subject first familiarized himself with the stereoscope, the phenomenon of binocular rivalry, and the use of the two microswitches to report the currently dominant stimulus. Next, with the conditions as described above for the movement trials, the absolute awareness threshold for the moving pattern was determined. This threshold was defined as the lowest intensity level (in terms of the value of the neutral density filter placed between the projector and stereoscope) at which the subject ever reported an awareness of being stimulated by the moving pattern during a threshold determination procedure (cf Dixon, 1971, p 12). The randomized double-staircase procedure described by Cornsweet (1962) was employed, the size of the 'steps' by which the intensity level was either decreased or increased corresponding to a value of 0.1 for the neutral density filter. In respect to this procedure the subject was given the following instructions: 'If you press the key in front of you and at the same time look into the apparatus you will see that I am presenting you with a moving pattern. What I shall do is sometimes present you with this, and sometimes not. What I want you to do is press the switch when I give you the signal and decide whether or not the moving stimulus is there. You do not actually have to see the whole pattern in motion, if you think you can see any movement, say "yes". The moving pattern is the only thing that will be presented.' Whilst undertaking this task the subject kept both eyes open but was asked to press the key whilst the red field was dominant.* The procedure advocated by Cornsweet was adhered to with the exception that a number of 'dummy' trials were included. For these trials one of the shutters in front of the projector was closed, preventing the superimposition of any light on to the red field. After the value of the projected light had levelled out, oscillating between two values over five successive trials in each of the two staircase series (cf Cornsweet, 1962) the procedure was terminated. A note was made of the lowest intensity level (highest value of neutral density

* the moving pattern was presented only to the right eye

filter) at which the subject reported the moving pattern to be present. For the trials involving the presentation of the pattern (moving or stationary) at a subliminal level, a 0.3 filter was added to the threshold-value filter. A corresponding reduction in the value of the filter ensured the supraliminality of the pattern in the supraliminal trials.

The subject next undertook the six trials of the experiment, each of which lasted 100 sec, in an order that was randomly selected from the four alternatives. The only proviso was that an equal number of subjects should undertake the experiment in each of the possible orders. Subjects were asked to report the rivalry alternations between the red and green fields by alternately closing the two microswitches. More specifically, they were asked to ignore the green rim which arose from the difference in size of the two fields, and to press the switch in their left hand whenever and for as long as the green field was dominant, and to press the switch in their right hand whenever and for as long as the red field was dominant. Thus, dominance was defined in relation to the red and equivalent area of the green field. In this way, when an image such as is shown in Fig 2b occurred, it was defined as being red dominant, despite the appearance of the green rim. If the colour were to change to any other, subjects were requested to refrain from pressing either key, and to report the event to the experimenter at the end of the trial. The first ten seconds of each trial were allowed for the subject to settle down to observing the rivalry without the need to report the alternations. At the end of this period a short auditory signal indicated the start of the trial proper, and the need to use the two switches. A 1 min rest-period was given between each trial.

Finally, precautions were taken to detect those subjects for whom the subliminality of the stimuli in that condition was unreliable. To this effect, subjects were approached immediately following the subliminal block of trials with the question: 'you did see the movement, didn't you?' It was

intended that any subjects responding positively to this would be rejected from the experiment. Those subjects answering in the negative were nevertheless subjected to an interrogation at the termination of the session. They were asked, 'What do you think the experiment is about - what is it that I am interested in?' 'Did you see anything that you may not have expected to see?' 'On how many trials did I show you the moving pattern?' Subjects' answers to these questions were interpreted in terms of the degree to which they were aware of the true purpose of the experiment, and the extent to which this knowledge derived from an awareness of the supposedly subliminal stimuli.

Source	Dominant (20 subjects) D.F.	S.S.	S.S.	S.S.	Suppressed (24 subjects) D.F.	S.S.	S.S.	S.S.
Between subjects	19	395.05	1198.01	1329.17	23	249.63	411.96	11262.93
Order	3	94.66	102.82	174.73	3	48.38	38.65	2998.41
Between subjects within groups (Error)	16	300.39	1095.19	1154.44	20	201.25	373.31	8264.52
Within subjects	100	488.59	1896.56	2142.69	120	137.98	233.07	9999.32
Threshold	1	56.56	358.63	381.62	1	13.73	0.92	875.11
Threshold x Order	3	1.14	2.74	60.04	3	3.68	2.64	447.91
Threshold x Error	16	114.13	185.41	257.03	20	39.17	50.64	2178.87
Condition	2	17.67	260.73	269.01	2	9.02	13.24	1097.04
Condition x Order	6	3.39	19.41	53.92	6	5.12	17.27	631.29
Condition x Error	32	114.34	372.75	300.76	40	22.86	66.44	2132.40
Threshold x Condition	2	26.96	251.31	400.43	2	8.61	4.08	623.80
Threshold x Condition x Order	6	36.69	11.72	59.71	6	3.73	5.34	406.42
Threshold x Condition x Error	32	117.71	433.86	360.17	40	32.06	72.50	1606.38
Total	119	883.64	3094.57	3471.86	143	387.61	642.50	21262.16

Results of analyses of variance applied, in order, to the mean dominance times for green, the mean dominance times for red, and the number of alternations for the dominant and suppressed conditions.

('Order' refers to the different orders of doing the six trials. 'Threshold' refers to the supraliminal/subliminal factor. 'Condition' refers to the blank/stationary/movement factor; cf. text.)

Table 1

		Dominant			Suppressed		
		Blank	Stationary	Movement	Blank	Stationary	Movement
Overall mean for dominance times of green field	Supraliminal	3.27	5.00	5.61	2.63	1.65	1.80
	Subliminal	3.58	3.11	3.07	2.70	2.91	2.32
Overall mean for dominance times of red field	Supraliminal	3.56	10.42	8.75	4.36	4.17	3.33
	Subliminal	4.07	4.11	4.17	4.39	4.00	3.95
Overall mean for number of alternations	Supraliminal	15.05	8.05	7.95	14.63	20.13	26.42
	Subliminal	13.45	14.20	14.10	15.00	14.75	16.63

The overall mean dominance times (in sec.) for the two rivalling fields, and the overall mean number of alternations, that emerged from the blank, stationary and movement conditions (cf. text).

(The stimuli, that were superimposed upon one of these fields being at subliminal or supraliminal levels and made contingent upon the field's dominant or non-dominant (suppressed) status.)

Table 2

RESULTS AND ANALYSIS

Though three subjects were unable to complete the experiment due to their extreme eye dominance, none had to be rejected as a result of the interrogation concerning the subliminal condition. That is, no subject reported being aware of the stimuli that were superimposed on the red field in the subliminal trials. Owing to an administrative error, however, the number of subjects undertaking the experiment in the dominant condition was four short of the intended 24. Data from 20 subjects were deemed sufficient.

Separate analyses of variance for repeated measures were applied to the average duration of the dominance phases of the two fields, in both the dominant and suppressed conditions. Similar analyses were also undertaken on the number of alternations. The resulting ANOVA tables were presented in Table 1, and the data are tabulated in condensed form in Table 2. The appropriate multiple comparisons confirmed the significance of a number of effects.

Effects resulting from the presentation of the moving pattern

For the movement condition the multiple-comparison tests (which involved contrasting the movement and stationary trials) failed to assign significance to any of the differences in the dominat condition for either subliminal or supraliminal presentation. This failure is consistent with the interpretation of Levelt's thesis. In contrast, in the suppressed condition both supraliminal and subliminal presentation has significant effects. In the latter case the mean dominance time of the green field was reduced ($F = 5.22$; $df = 1, 40$; $P < 0.05$), whilst the mean dominance of the red field remained unaffected. With the increase in the number of alternations in this condition (which, however, failed to attain significance) the results again conform to the predictions based upon Levelt (1966). For the supraliminal presentation of the moving pattern the predicted increase in alternation rate was observed ($F = 11.83$; $df = 1, 40$; $P < 0.05$), though this arose from a reduction in the mean dominance time of the red field ($F = 4.68$; $df = 1, 40$; $P < 0.05$) and not the green field as

predicted. Though inconsistent with the predictions, subjects' introspective reports did suggest that Levelt's thesis was inapplicable to this condition. Thus, the appearance of a composite image was reported, in which the superimposed red pattern was seen to move 'through' or 'above' the contralateral green field. Clearly, this makes for difficulties in the interpretation of subjects' responses in this condition, in addition to precluding the application of Levelt's thesis.

Effects resulting from the presentation of the stationary pattern

Multiple comparison tests that involved contrasting the stationary and blank conditions failed to reveal any effects arising from the presentation of the stationary pattern at subliminal levels. In contrast, presentation at a supraliminal level did influence the rivalry alternations. Conforming to the predictions (it is assumed that the pattern added to the stimulus strength of the red field), the effects in the suppressed condition centred on the mean dominance time for the green field. This mean was found to be significantly reduced ($F = 14.35$; $df = 1, 40$; $P < 0.05$), causing an increase in the alternation rate ($F = 9.04$; $df = 1, 40$; $P < 0.05$). In the dominant condition, and this was not predicted, the mean times of dominance of both the green and red fields increased ($F = 8.13$; $df = 1, 32$; $P < 0.01$; and $F = 34.7$; $df = 1, 32$; $P < 0.05$, respectively), giving rise to a reduction in the alternation rate ($F = 42.3$; $df = 1, 32$; $P < 0.05$).

Due to the confounding of effects arising from the increase in luminance and from the pattern per se the results from this section should not be given too much weight. The results of a stochastic analysis of the rivalry alternations in the blank condition (the purpose served by the inclusion of this condition) are to appear in a later chapter.

DISCUSSION

With regard to the conditions of central interest, involving the subliminal presentation of the moving pattern, the propositions outlined in the introduction were supported.

(a) Movement can be discriminated under conditions that prevent the subject from being aware of the stimulus. In the suppressed condition, two factors served to ensure this lack of awareness. Firstly, presentation of the moving pattern was made to coincide with the phases of non-dominance of the field upon which it was superimposed. Secondly, the 'energy level' of the stimulus was reduced sufficiently for it to qualify as subliminal. This qualification was justified with the satisfaction of two criteria (cf Dixon, 1971). Firstly, the stimulus was presented below the predetermined awareness threshold, where this threshold was defined as the lowest level of stimulus energy at which the subject ever reported seeing anything of the stimulus during the whole of the threshold determination procedure. Secondly, subjects reported retrospectively that they saw nothing of the stimulus, in either the suppressed or dominant conditions.

(b) The discrimination of movement is possible for a stimulus that is, in the context of binocular rivalry, currently non-dominant. Not only was the temporal course of rivalry found to be sensitive to the presence of a moving pattern within the currently non-dominant field, but the nature of the effects confirmed Levelt's thesis under conditions that favour its literal interpretation. Generalizing from this, it is proposed that any features that contribute to the strength of a stimulus, thereby influencing the course of rivalry in accordance with Levelt's thesis, are discriminated by the visual system whilst they are non-dominant, or phenomenally 'suppressed'.

(c) The discrimination of movement in a non-dominant field is possible even for a stimulus that is otherwise subliminal.

(d) Finally, in confirming the literal interpretation of Levelt's thesis, the results suggest that the non-dominant stimulus is not only capable of influencing the perceptual alternation process that characterizes rivalry, but actually takes precedence in this.

3.2 EXPERIMENT 2 THE SUBLIMINAL PERCEPTION OF MOVEMENT AND THE COURSE OF AUTOKINESIS: CONFIRMATION OF THE FINDINGS OF EXPERIMENT 1

To the author's knowledge, Experiment 1 is the only demonstration that the movement of a subliminal stimulus may be discriminated. Since the implications of the findings from Experiment 1 are important for the present thesis, a further study was undertaken in an attempt to confirm that a subject is capable of discriminating the movement of a subliminal stimulus. The course of autokinesis was selected as the dependent variable, since it is known to be particularly sensitive to the presence of additional information in the visual field (cf Royce et al, 1966). Thus, it was asked whether the course of autokinesis would be sensitive to the real movement of a surrounding pattern that was presented at a subliminal level. Studies of induced movement (cf Wallach, 1959) would lead us to anticipate such sensitivity in the case of the supraliminal presentation of real movement.

Method

Subjects restricted themselves to reporting the apparent upward and downward movement of a spot-source of light. Apparent movement in a horizontal direction was ignored, so that, for example, the subject was instructed to regard apparent movement of the spot in a diagonally-upward direction as upward movement.

Each subject completed three trials during which he reported the vertical component of the autokinetic movement. The trials were distinguished by the condition of a pattern that was projected on to a perspex screen immediately behind and surrounding the spot source of light. For the main group of eighteen subjects this pattern was always subliminal (as defined below), but on any trial was either moving vertically upward (upward condition), vertically downward (downward

condition), or was stationary (stationary condition). An equal number of subjects completed the three trials in each of the six possible orders. From the data recorded on each trial, the following could be calculated: the mean duration for which the spot appeared to move, without interruption, in an upward (downward) direction, the mean duration for which the spot remained stationary, the frequency and total duration of each of these response states; the mean duration of continuous apparent movement, regardless of the direction of this movement.

A further group of just six subjects undertook the same task with the pattern presented at a level above the awareness threshold. Each of these subjects completed the three trials in a different order.

Apparatus

A 10 milliamp, micro-lamp, that was mounted inside a small cylinder that had only a pin-hole in the edge facing the subject, served as the stimulus for the autokinetic effect. This cylinder was fixed against the centre of a translucent perspex screen (0.4m diameter) which was let into an otherwise opaque frame that rested on the floor. The screen was situated 1m from the seated subject, and the moving pattern was projected on to it by passing the edge of a rotating transparent disc through the focal plane of an Aldis Tutor 1000 projector. Commercial Letratone, Pattern LT 100 (cf Fig 2), was applied to the disc. Viewed from this distance, the projected pattern traversed a linear path, with a velocity of 20 deg $sec.^{-1}$ The irregular and fine texture of the pattern ensured that no fluctuation in gross intensity accompanied the movement, and that the pattern never took on a striped appearance. For the stationary condition the transparent disc was prevented from rotating, whilst for the upward and downward conditions the disc was made to rotate in opposite directions.

The experiment was undertaken in a light-proof cubicle, and the projector, motor, and disc were positioned inside a thick, opaque enclosure, Sufficient light strayed, however, for fully dark-adapted subjects to be aware of the translucent perspex screen. The pattern, therefore, was projected on to an otherwise dimly-illuminated screen.

A series of Kodak Wratten neutral density filters was placed in front of the projector lens. The critical effect of interposing a filter in this way was to decrease the contrast of the projected pattern.

Two microswitches were provided for the subject to report the vertical component of the autokinetic movement, and each 'switch' was connected to one channel of an Esterline Angus multiple-channel pen-recorder.

Subjects

Ten male and fourteen female undergraduate students, ages 19 - 23 years, served as subjects; none were students of psychology.

Procedure

The three experimental trials were preceded by a period of dark adaptation that lasted 25 minutes. The absolute awareness threshold for the moving pattern, as defined and assessed in Experiment 1, was then determined. In respect of threshold determination the subject was given the following intructions: "When instructed, open your eyes and look at the screen in front of you. What I shall do is sometimes present a moving pattern on the screen, and sometimes not. What I want you to do is each time decide whether or not the moving stimulus is there. You do not actually have to see the whole pattern in motion; if you think you can see any movement, say "yes". The moving pattern is the only thing that will be presented". In order to avoid

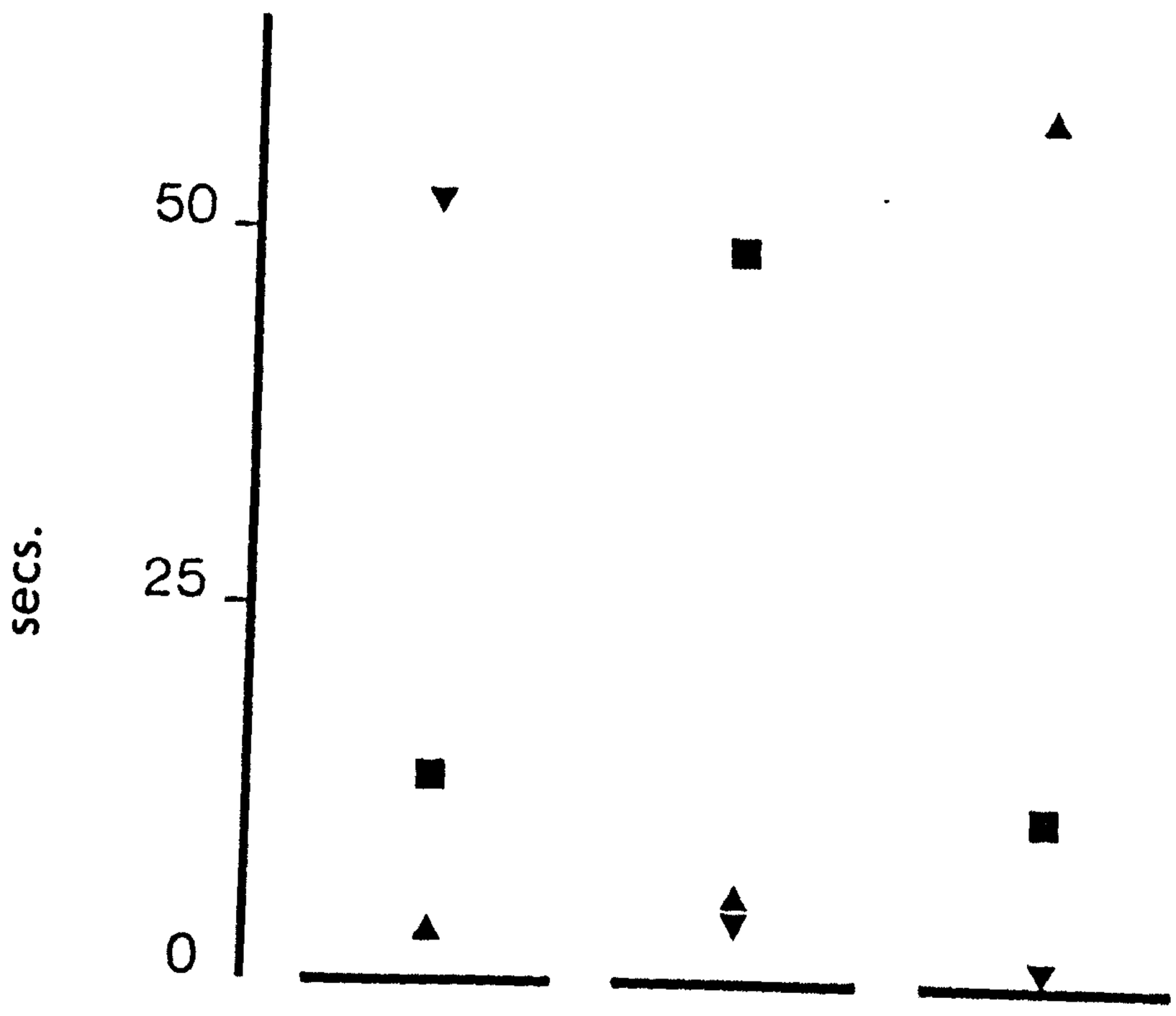
their seeing the neutral density filters being changed, subjects were also asked to close their eyes between trials. As for Experiment 1, for trials involving the presentation of the pattern (moving or stationary) at a subliminal level, a 0.3 filter was added to the threshold-value filter. A corresponding reduction in the value of the filter ensured that the pattern was supraliminal when this was appropriate.

The subject next undertook the three trials of the experiment, each of which lasted 4 min, in an order that was randomly selected from the six alternatives. Subjects were asked to report the vertical component of the apparent movement by alternately closing the two microswitches. More specifically they were asked to press the switch in their left hand whenever and for as long as the spot appeared to move upward, and to press the switch in their right hand whenever and for as long as the spot appeared to move downward. When there was no vertical movement the subject was instructed to refrain from pressing either switch. The end of each 4 min period was indicated to the subject by a short auditory signal, and this was followed by a 30 sec rest-period during which the subject closed his eyes.

Finally, precautions were taken to detect those subjects for whom the subliminality of the pattern, in that condition, was unreliable. To this effect subjects were approached immediately following the three experimental trials with the question: "You did see the moving pattern, didn't you?" It was intended that subjects answering positively to this question would be rejected from the experiment. Subjects answering in the negative were nevertheless subjected to a further interrogation, being asked: "What do you think the experiment is about - what is it that I am interested in?" "Did you see anything that you may not have expected to see?" "On how many trials, and which trials did I show you the moving pattern?" A subject's answers to these additional questions were interpreted in terms of the degree to which they indicated that he was aware of the true purpose of the experiment, and the extent to which this knowledge derived from an awareness of the supposedly subliminal stimulus. In the event, these additional questions were unnecessary.

Figure 4

Averaged over subjects, the mean duration for which the spot of light appeared, during a trial, to move up (▲), remain stationary (■), and move down (▼) without interruption, when the surrounding pattern was presented at a supraliminal level and made to move upwards, remain stationary, or move downwards.


50
25
0
secs.
condition of pattern
up
stationary
down

Source	D.F.	S.S.	M.S.	F	S.S.	M.S.	F
Between subjects	5	6.60	1.32		105678	21135	
Within subjects	12	650.39	54.2		36147	3012	
Condition	2	297.62	148.8	4.2	12662	6331	2.697
Condition x Subjects	10	352.72	35.3		23484	2348	
Total	17	656.98			141825		

For the supraliminal condition, the results of the analyses of variance applied, in order, to the values for the difference between the mean duration of continuous upward and downward apparent movement on any trial (after square root transformation), and to the values for the total time during a trial for which the spot remained stationary.

("Condition" refers to the three experimental conditions)

Table 3

RESULTS AND ANALYSIS

None of the subjects had to be rejected from the experiment as a result of the interrogation concerning the subliminal stimulus; that is, all subjects gave a negative reply to the first question and remained consistent with this in answering the additional questions. Thus, they were unable to guess the purpose of the study, did not see anything other than a homogeneous screen and spot of light, and finally were unable to offer an answer to the last question.

After transforming the data where necessary to ensure homogeneity of variance and normality of within treatment distributions, analyses of variance with multiple comparisons were employed. However, where these pre-requisites could not be satisfied, non-parametric tests were utilized.

Effects from the supraliminal presentation of movement

With regard to the mean duration of continuous apparent movement in a particular direction, a comparison of subjects' responses in the two trials involving the moving pattern demonstrated that this was relatively longer for apparent movement in the direction opposite to the real movement. From each trial, the difference between the mean duration of continuous upward movement and the mean duration of continuous downward movement was determined. After their square-root transformation, the difference scores for the two movement conditions were found to vary significantly ($F = 8.43$; $df = 1,10$; $P < 0.025$), cf Fig 4 and Table 3. In addition, the presentation of movement, in either direction, encouraged autokinesis by reducing the total time during a trial in which there was a cessation in the apparent movement ($F = 5.02$; $df = 1,10$; $P < 0.05$), cf Table 3.

Figure 5

Averaged over subjects, the mean duration for which the spot of light appeared during a trial to move up (▲), remain stationary (■) and move down (▼) without interruption, over successive subliminal trials. Results from subjects who first undertook the upward (- - - -), stationary (————) or downward (--- · ---) condition. Note, for the second and third trials the distinction between the three experimental conditions is not maintained.

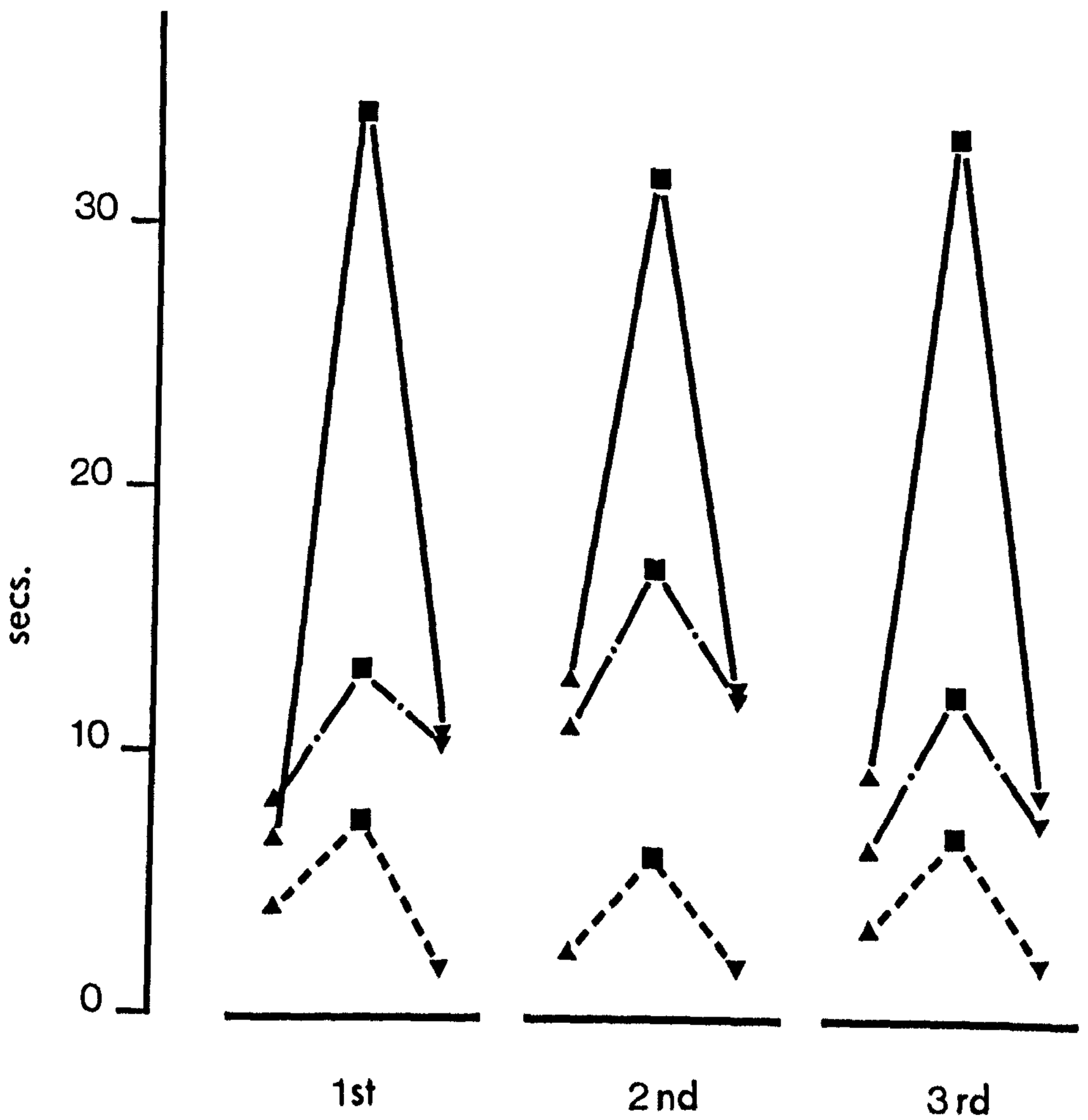
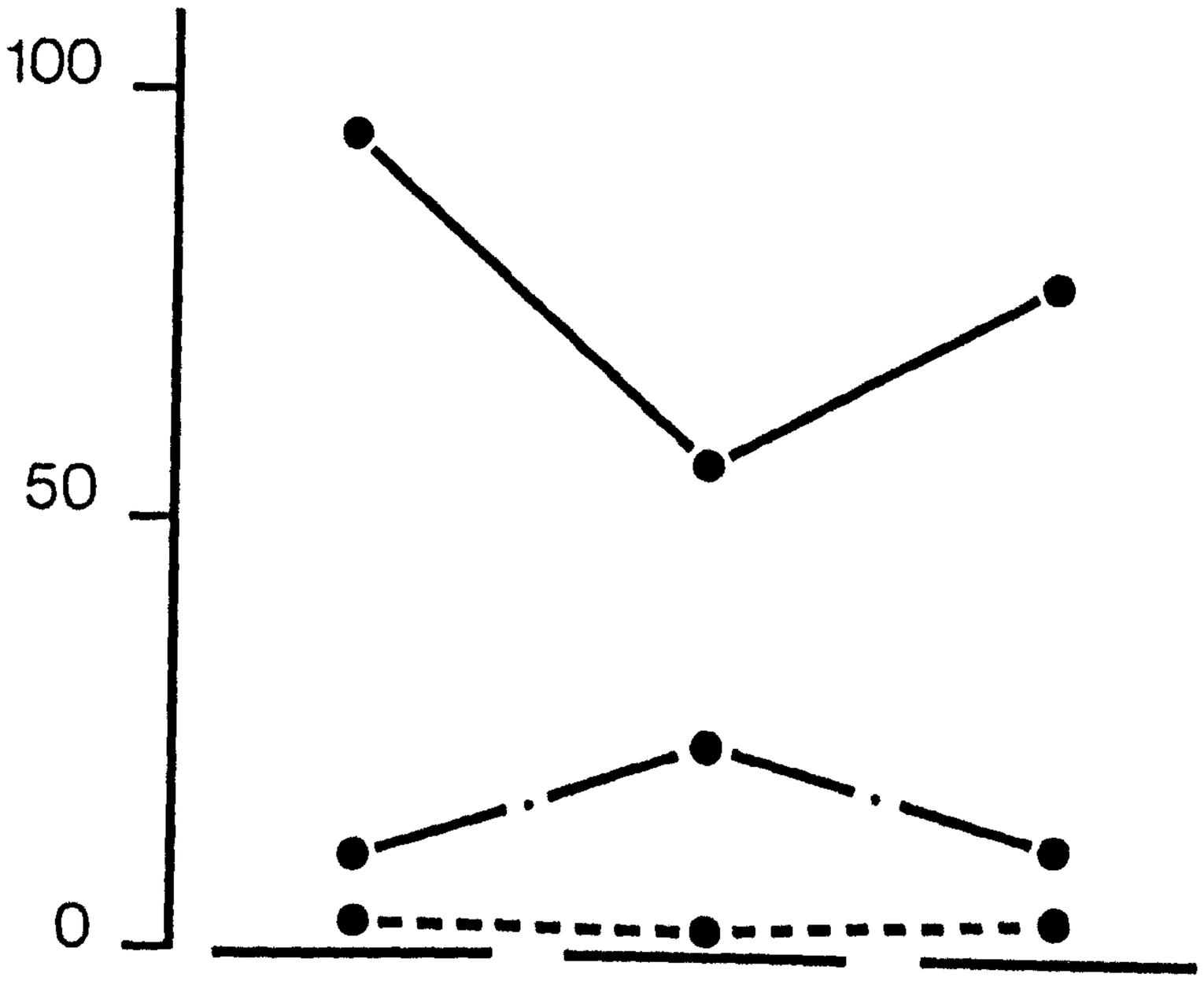

30
20
10
0
secs.
1st
2nd
3rd
Trial

Figure 6

For successive subliminal trials, the
mean duration of continuous apparent movement,
direction ignored, cf. Fig. 5 for code.


100
50
0
1st
2nd
3rd
Trial

Condition						
Upward (subjects 1-6)	30	16	30	9	51	26
Stationary (subjects 7-12)	1	1	23	7	1	18
Downward (subjects 13-18)	8	19	9	8	12	18

For the six subjects in each of the three conditions of experiment 2, the frequency of the stationary phases on the first subliminal trial.

Table 4

Condition						
Upward (subjects 1-6)	1.00	0.81	0.89	0.89	0.83	0.93
Stationary (subjects 7-12)	0.00	0.00	0.83	0.35	0.00	0.95
Downwards (subjects 13-18)	1.00	0.63	0.89	0.26	1.00	0.88

For the six subjects in each of the three conditions of experiment 2, the probability that a movement phase would be immediately followed by a stationary phase rather than by movement in the opposite direction on the first subliminal trial.

- Table 5

Source	D.F.	S.S.	M.S.	F	S.S.	M.S.	F	S.S.	M.S.	F
Condition	2	145	72.9	1.89	0.88	0.44	5.24	4.21	2.10	6.00
Error	15	579	38.6		1.26	0.08		5.21	0.35	
Total	17	725			2.14			9.42		

For the subliminal condition, the results of the analyses of variance applied, in order, to the difference between the mean duration of continuous upward and downward movement, the mean duration of the stationary phases (after log. transformation) and the mean duration of continuous apparent movement in any direction (after log. transformation).

Table 6

Effects from the subliminal presentation of movement

The most immediate pattern emerging from the results indicated that the course of autokinesis on trials subsequent to the first simply reflected the course of apparent movement arising on the first trial, cf Fig 5,6. Taking this finding into account, statistical testing for the effects of the experimental variable was confined to the data arising on the first trial.

Contrary to the effects of movement at a supraliminal level, in this condition there was no significant tendency for the moving pattern to induce movement in the opposite direction. When an analysis was undertaken on the values for the difference between the mean duration of continuous upward apparent movement and the mean duration of continuous downward apparent movement, the two movement conditions did not differ significantly ($F = 2.09$; $df = 1, 15$; $P > 0.05$), cf Table 6 and Fig 5. However, it was revealed that with the presentation of movement, in either direction, the stationary phases of autokinesis were more frequent (Mann-Whitney $U=14$; $P < 0.05$, two-tailed) and reduced in mean duration ($F = 8.68$; $df = 1,15$; $P < 0.01$ after log. transformation), cf Tables 4, 6 and Fig 5. As would be expected from this change in the frequency of the stationary phases, the movement of the surrounding pattern gave rise to a decrease in the mean duration of continuous apparent movement, when the direction of this movement was ignored ($F = 7.79$; $df = 1,15$; $P < 0.025$, after log. transformation), cf Table 6 and Fig 6. Finally, the mean duration of continuous apparent movement was not significantly changed by the presence of movement when either apparent movement upwards or apparent movement downwards are considered separately.

From this pattern of significant results, the critical effect of the movement of the subliminal pattern would appear to be the induction of stationary phases, of shorter duration than the stationary phases observed when the pattern is stationary, at a time when autokinesis is changing direction. Looking at a rather different aspect of the results confirms this. Given in Table 5 are the values, derived from each subject's first trial, for the probability that a period of autokinetic movement, in a particular direction, would be

followed by a period of "stationarity" before appearing to move in the opposite direction. A Mann-Whitney U test that compared the two movement conditions against the stationary condition revealed that, with the presentation of the moving pattern, periods of autokinetic movement in a particular direction are more likely to be immediately followed by a stationary phase than by movement in the opposite direction ($U = 14$; $P < 0.05$, two-tailed).

Introspective reports

Subjects in the subliminal condition reported that the dimly illuminated screen that surrounded the spot source of light, spontaneously disappeared and reappeared. More importantly, however, these subjects also reported that the periods of apparent movement of the spot of light coincided with the disappearance of the surrounding screen. During the post-experimental interrogation, a number of subjects suggested that the purpose of the experiment was to investigate the relationship between the movement of the light and the presence of the surrounding frame.

DISCUSSION

The results demonstrate that the course of autokinesis is sensitive to the real movement of a surrounding pattern, even when this pattern is presented at a subliminal level. Consistent with Wallach's (1959) observations, movement in a direction opposite to that of the real movement was induced when the surrounding pattern was presented at a supraliminal level. In the subliminal condition, movement of the pattern served to induce periods of stationarity between the phases of upward and downward apparent movement. These periods were relatively brief compared to those observed in control conditions. These preliminary observations, therefore, confirm that the movement of a subliminally-presented stimulus may be discriminated.

A tentative explanation of the nature of the effects in the subliminal condition may be suggested, on the basis of subjects' reports that these periods of stationarity coincided with periods when the surrounding screen was perceived. These reports suggest that the effects were mediated indirectly, via the effect that the real movement had on the behaviour of the image of the screen. When visible, this image would act as an inhibiting framework and so, if it is considered that the occurrence of apparent movement is incompatible with the appearance of a surrounding framework, it would seem reasonable that the screen should reappear when there is a momentary cessation in autokinesis as the direction of movement changes. That the image of the screen should have disappeared is understandable (cf Evans, 1973) since the steady fixation of large stimuli under conditions of dim illumination gives rise to the phenomena that are typically obtained with more rigid stabilizing procedures (cf also Evans & Piggins, 1963). If it is assumed that images behave in a similar manner in rivalry and under stabilized viewing conditions (cf Chapter 6 below), some support for this tentative explanation comes from Experiment 1, where it was found that superimposing a moving, subliminal pattern on a homogeneous field served to reduce the period for which the field disappeared.

Finally, the unexpected observation that the course of autokinesis on the second and third trials in the subliminal condition simply

reflected the course of the first trial, is difficult to explain. It may be suggested that subjects generated expectations as to the course the apparent movement would take, and that these expectations later governed the observed pattern of autokinesis. That the phenomenon is very much determined by a subject's expectations has been demonstrated (Sherif, 1935 and Rechtschaffen & Mednick, 1955).

To summarize, these results confirm that the movement of a subliminally-presented stimulus may nevertheless be discriminated.

3.3 EXPERIMENT 3 A RESPONSE TO THE MEANING OF A SUPPRESSED SUBLIMINAL STIMULUS, AND ITS HABITUATION

An unsuccessful study, in which an attempt was made to show that the 'meaning' of a stimulus might influence the course of binocular rivalry, shaped the design of this third experiment. In the pilot study, words and control stimuli (the same words whose letters had been dissected and the fragments rearranged) were superimposed on a rivalling field under the conditions of presentation employed in the movement study. One change in design involved the alternate presentation of control and experimental stimuli over successive trials. Thus, each subject undertook eight trials involving the alternate presentation of one of four experimental, and one of four control stimuli. Upon consideration of the results it was thought that two factors may have been responsible for the failure of the study. Firstly, it was considered that any differential response to the meaning of the experimental stimuli may have been masked by the response to the selective information content of each stimulus, experimental and control alike. Because of the alternation between successive experimental and control stimuli, every presentation involved a relatively novel type of stimulus. Indeed, in this respect, it may be thought that the control simuli, by virtue of their unfamiliarity, would add the most to a field's stimulus strength. Secondly, having just one experimental trial between each control may have been inappropriate, particularly in the subliminal conditions, since there is evidence that responses toward a subliminal stimulus are most prominent on the second successive presentation of a stimulus (Silverman, 1971).

With these considerations in mind, an experiment was designed in a further attempt to determine whether the meaning of a stimulus may be discriminated when it is presented within the currently non-dominant field in binocular rivalry. More specifically, it was asked whether the introduction of a word (as opposed to a meaningless control) into such a field would reduce the amount of time for which it remained non-dominant. Again

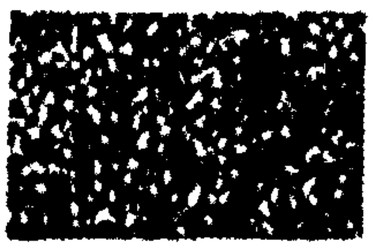
reference was made to Levelt's (1966) thesis, under the assumption that, as did movement, meaningfulness would serve to increase the 'stimulus strength' of the field upon which it was superimposed. The effect on the course of rivalry would be expected to accord with Levelt's thesis. Again, different conditions of stimulus presentation were employed in order to test the literal form of Levelt's thesis. Thus, the presentation of control and experimental stimuli to a rivalling field was restricted to coincide with either its non-dominant or dominant phases. As in the movement study, a condition that involved the subliminal presentation of the stimuli was incorporated in the design, in order to again determine whether the aspect of the visual system that is capable of responding to information in the no-dominant field is also capable of mediating subliminal perception. In addition, in view of the failure of the pilot study, the following hypotheses were also put to the test: (i) that the appearance of a differential response to the meaningful content of the experimental stimuli would be dependent upon the subject's prior habituation toward the control stimuli, and (ii) that any effects in the subliminal conditions would be greatest on the second successive presentation of an experimental stimulus.*

Finally, one problem that was encountered in the pilot study related to the fact that, compared to the coloured circular fields of the stereoscope, the words were relatively small. To avoid the possibility that this would encourage a piecemeal form of rivalry, in which the area covered by the word and its contralateral equivalent would rival independently of the rest of their coloured fields, relatively small, achromatic rivalling stimuli were employed in the present study.

* Indeed, any effects may only be observed on the second presentation.

Figure 7

The achromatic rivalling fields employed in experiment 3. The "random-texture" stimulus was presented to the subject's left eye, and the open rectangle, within which additional stimuli were projected, was presented to the right eye. The stimuli were positioned so as to appear concentric.



Method

Each subject reported the alternations between the two achromatic rivalling fields illustrated in Fig 7. The selection of these stimuli followed informal experimentation whose aim was to find two quite distinct stimuli that would display an unambiguous rivalry and yet allow the projection of an additional stimulus on to a homogeneous portion of one of the fields. The open rectangle was presented to the subject's right eye and it was within this that the additional stimulus was superimposed. The two fields were arranged in the stereoscope so as to appear 'concentric'.

Variation* of the stimulus conditions involved changes to the right field. The fourteen trials undertaken by each subject were segregated into two blocks, according to whether the number of control trials (trials involving the presentation of control stimuli) that preceded two successive experimental trials (trials involving the presentation of a meaningful, experimental stimulus) was seven or three. Thus, the two blocks of trials were arranged C1-C2-C3-C4-C5-C6-C7-E1-E1, or C1-C2-C3-E1-E1; where C1-C7 are seven different control stimuli, and E1-E1 represents successive presentations of the same experimental stimulus. An equal number of subjects, in each condition, completed the two blocks of trials in the two orders that were possible. When stimuli were superimposed on the right field, their presentation was made contingent upon whether the right field was reported to be currently dominant (dominant condition) or currently non-dominant (suppressed condition). Moreover, the stimuli were presented at either a supraliminal or subliminal (as defined below) level. Thus, there were four conditions of presentation: suppressed/subliminal; suppressed/supraliminal; dominant/subliminal; dominant/supraliminal. Independent groups of subjects were employed with respect to these conditions.

From the data recorded on each trial the number of alternations and average duration of dominance of each field could be calculated.

* right eye field

Figure 8

Examples of the experimental and control stimuli employed in experiment 3. Each of these stimuli would, at different times, be projected to subject's right eye so as to appear inside the open rectangle.

GANDER

Apparatus

The apparatus was essentially the same as in the movement experiment. However, the red and green filters were removed and the two rectangles applied directly to the semi-transparent tracing-film screens. Both rectangles appeared within circular fields that subtended 10deg. The randomly-patterned rectangle was constructed from commercial Letratone, Pattern LT 100, subtended 7.5 by 4.5deg and was presented in the left field. The line rectangle was drawn on the tracing-film screen in black ink and subtended 5.5 by 2.0deg. The lighter parts of each field had their illuminance measured at 1.0 lof ft lamberts. Additional changes involved the removal of the circular disc from the focal plane of the projector, and its replacement by the original slide holder.

The words that were used as experimental stimuli were selected from a report of a previously successful experiment that had involved their presentation at a subliminal level (cf Hardy and Legge, 1968). These words were printed in Letraset, later photographed and the negatives mounted as slides. The control stimuli were constructed by separating the top and bottom halves of each letter and rearranging the fragments on a random basis. One of these words, together with one of its controls, is illustrated in Fig 8. There were four words chosen, each having relatively neutral meaning (cf Hardy and Legge, 1968). They were GANDER,FENCER, FEATURE, PLASMA. From each of these words three different control stimuli were constructed.

When projected on to the right field, each stimulus fitted snugly into the line rectangle and subtended 4.5 by 0.8deg visual angle.

Two microswitches were again provided for the subject to report the rivalry alternations. With one switch connected to a camera shutter mounted in front of the projector, the presentation of the stimuli was restricted to the dominant or non-dominant phases of the right field.

Subjects

Forty subjects took part in the experiment. All were undergraduate students at University College, London: none were students of psychology.

Procedure

In most respects the procedure was as in Experiment 1. The subject familiarized himself with the stereoscope, the phenonenon of binocular rivalry, and the use of the two switches to report the currently dominant stimulus. Next, the absolute awareness threshold for a test stimulus (the word FINGER), as used by Hardy and Legge, 1968) was determined. This threshold was again defined as the lowest intensity level (in terms of the value of the neutral density filter placed between the projector and stereoscope) at which the subject ever reported an awareness of being stimulated by the test stimulus during a threshold determination procedure. The threshold determination procedure and instructions were as in the movement study. Again, for the trials involving the presentation of the stimuli at a subliminal level, a 0.3 filter was added to the threshold-value filter. A corresponding reduction in the value of the filter ensured the supraliminality of the pattern in the supraliminal trials.

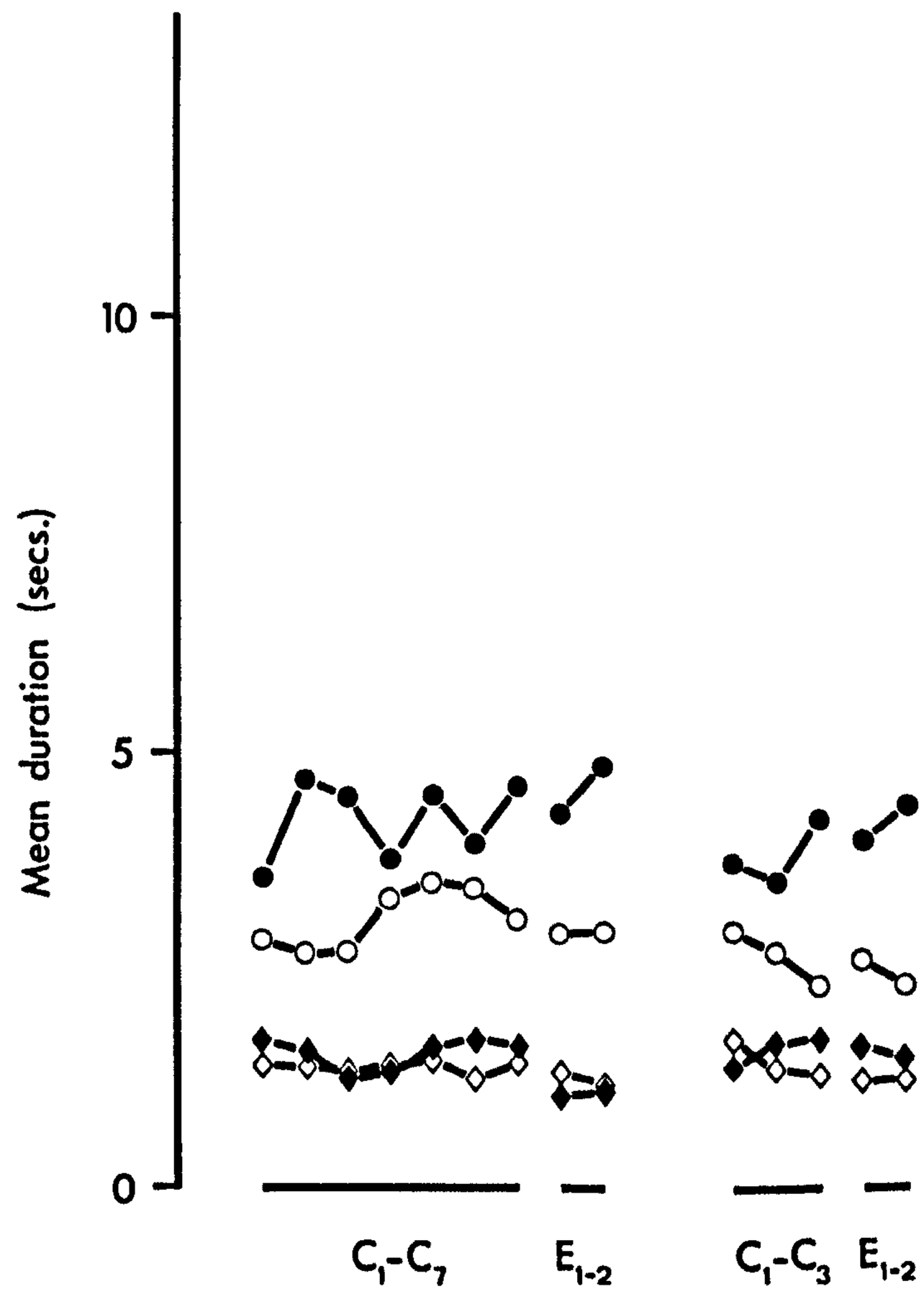
It was next determined, on a random basis, under what condition and in which order the subject would undertake the fourteen trials of the experiment, each of which lasted 60 sec. The only proviso was that ten subjects should undertake each condition, and an equal number of these should complete the longer and shorter series of control trials first. For the control trials for each subject, ten different control slides were randomly selected from the pool of twelve. In a similar manner, two of the four experimental slides were chosen to serve as the experimental stimuli, one of these being used after the longer series of control trials and one after the shorter series.

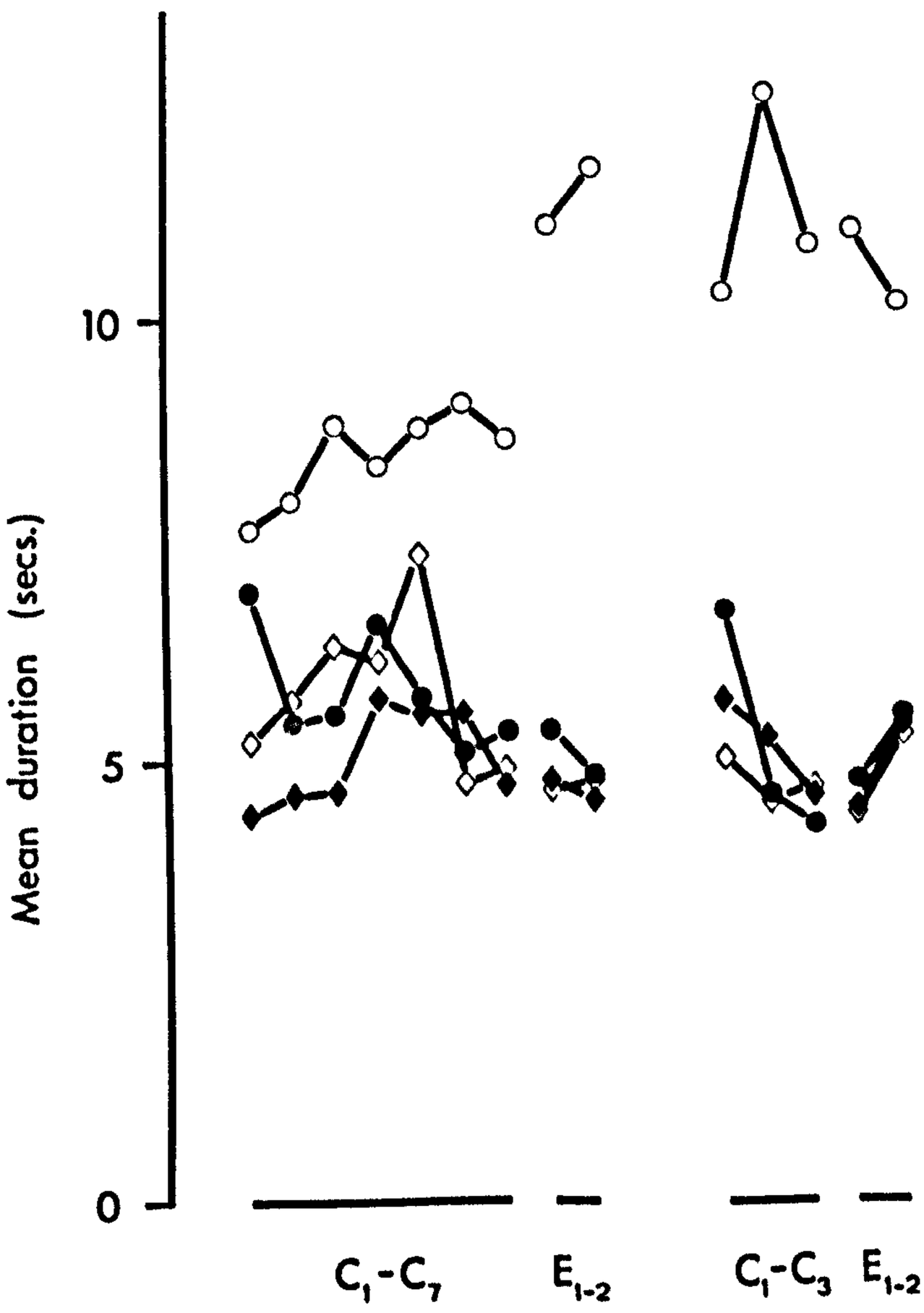
Subjects were asked to report the rivalry alternations by pressing the switch in their left hand whenever and for as long as the randomly-constructed rectangle was dominant, and to press the switch in their right hand whenever and for as long as the line rectangle was dominant. A one-minute rest-period was given between each trial and a five-minute rest-period between the two blocks of trials.

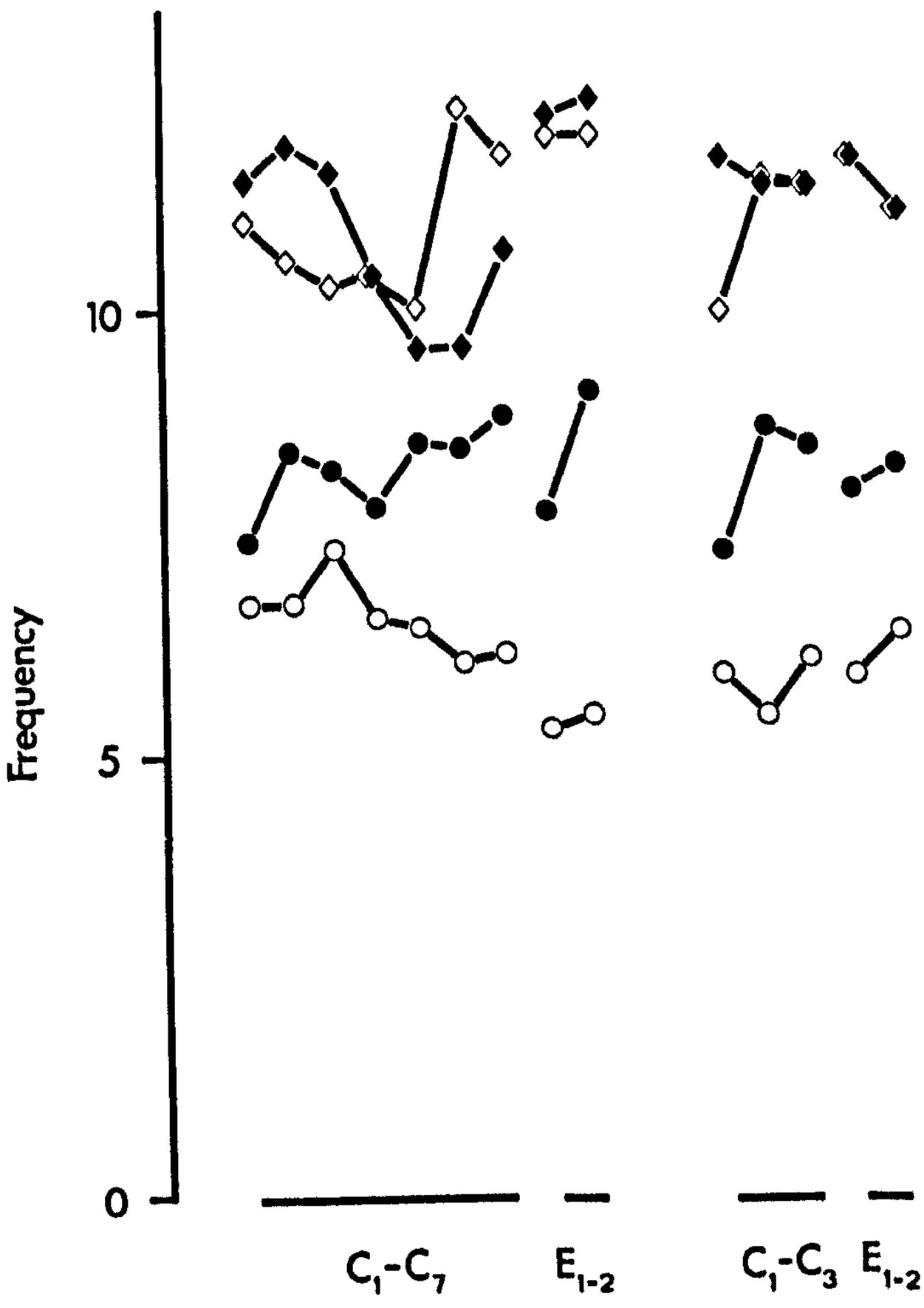
Finally, precautions were again taken to detect those subjects for whom the subliminality of the stimuli in that condition was unreliable. Thus, immediately after the experiment, subjects were asked a similar series of questions to those used in the movement study.

Figure 9 a,b,c

The mean values, averaged over subjects and order of presentation, for the mean duration for which the right field was non-dominant (Fig. 9a), was dominant (Fig. 9b), and for the number of alternations (Fig. 9c).
C1-C7 and C1-C3 represent successive control trials, and E1-E1 represent successive experimental trials.
◆, ◇, ● and ○ represent the suppressed/subliminal, suppressed/supraliminal, dominant/subliminal, and dominant/supraliminal conditions respectively.


10
5
0
Mean duration (secs.)
C1-C7
E1-2
C1-C3
E1-2
Trials


10
5
0
Mean duration (secs.)
C1-C7
E1-2
C1-C3
E1-2
Trials


10
5
0
Frequency
C1-C7
E1-2
C1-C3
E1-2
Trials

SOURCE	D.F.	S.S.	S.S.	S.S.	
Within subjects (linear)	40	188.46	385.7	15.82	
T(linear)	1	0.86	0.35	0.98	
G x T(linear)	3	52.11	24.73	0.70	
O x T(linear)	1	4.76	9.02	0.65	a.
(G x O) x T(linear)	3	10.77	71.66	0.49	
Error x T(linear)	32	119.97	279.94	13.00	
Within subjects (linear)	40	157.00	245.06	20.77	
T(linear)	1	8.45	13.04	0.02	
G x T(linear)	3	10.65	23.43	4.01	
O x T(linear)	1	9.80	6.78	0.34	b.
(G x O) x T(linear)	3	3.70	18.64	1.82	
Error x T(linear)	32	124.40	183.17	14.58	

Linear trend components of the within subjects sums of square, relating to the data from the longer series of control trials (a) and the shorter series of control trials (b), and in order, to the number of alternations, the mean dominance times for the right field, and the mean dominance time for the left field.

'G' refers to the different conditions of stimulus presentation viz. suppressed/subliminal, suppressed/supraliminal etc.

'O' refers to the different trial orders for completing the experiment.

'T' refers to the seven (or three) successive control trials.

Table 7

Number of alternations

G_1	12.0	15.0	10.0	-5.0	24.0	12.0	8.0	0.0	7.0	7.0
G_2	-11.0	-1.0	-1.0	-8.0	0.0	1.0	-23.0	-12.0	3.0	-3.0
G_3	0.0	-27.0	5.0	-10.0	-6.0	24.0	-5.0	-21.0	1.0	-6.0
G_4	15.0	28.0	3.0	0.0	-4.0	-1.0	3.0	-2.0	-2.0	1.0

Mean duration of dominance of right field

G_1	-14.8	-2.0	0.2	1.6	-2.9	-4.3	-1.8	-0.5	-10.9	-1.6
G_2	12.3	4.8	-0.7	4.0	0.5	-6.9	1.9	0.5	-1.1	2.8
G_3	2.4	5.3	-5.3	14.9	4.4	-9.3	19.8	12.1	-3.3	10.1
G_4	-16.5	-88.1	5.9	-0.9	11.0	29.2	-4.5	1.6	2.7	7.5

Mean duration of dominance of left field

G_1	-0.2	-3.5	-3.4	4.5	-0.2	-1.3	-1.2	-0.4	2.0	-0.3
G_2	-1.6	-4.3	1.1	-0.2	1.3	-1.4	2.4	0.8	2.3	0.6
G_3	-2.0	3.8	-4.4	2.1	1.4	-8.3	2.0	-2.7	-6.7	-0.8
G_4	2.4	-0.0	-2.2	1.7	3.8	-9.6	-0.7	1.2	-5.5	-5.6

Values for the sum of squares due to linear trend for the longer series of control trials, for each subject and each parameter. The weighting coefficients employed were +3 +2 +1 0 -1 -2 -3 for trials 1-7.

G_1 - the suppressed/subliminal condition. G_2 - the suppressed/supraliminal condition. G_3 - the dominant/subliminal condition. G_4 - the dominant/supraliminal condition.

Table 8

Number of alternations

G_1	-3.0	3.0	3.0	-5.0	-1.0	4.0	-1.0	1.0	1.0	1.0
G_2	-1.0	-7.0	-4.0	-4.0	-1.0	6.0	1.0	-3.0	-1.0	-1.0
G_3	0.0	3.0	-6.0	-1.0	-4.0	1.0	0.0	-2.0	0.0	-3.0
G_4	0.0	0.0	2.0	3.0	-2.0	0.0	0.0	-1.0	-4.0	0.0

Mean duration of dominance of right field

G_1	4.8	-1.2	-0.4	8.9	0.2	-0.5	0.6	-0.3	-3.0	1.7
G_2	0.5	1.2	0.8	5.0	1.5	-7.1	-0.8	1.5	0.0	0.6
G_3	0.9	-1.3	9.0	3.0	5.6	1.2	-0.7	0.5	2.8	2.9
G_4	-0.6	0.0	-0.9	-6.0	9.2	-3.9	-1.9	0.3	0.8	-2.6

Mean duration of dominance of left field

G_1	-0.3	-0.2	-0.4	-0.5	0.0	-0.8	-0.2	0.0	0.0	-0.4
G_2	-0.1	1.5	0.8	0.4	-0.1	0.6	0.5	-0.4	0.4	0.2
G_3	-0.8	-0.1	0.9	-1.6	-0.2	-1.9	0.8	0.3	-2.8	0.1
G_4	0.6	0.0	-0.6	-0.3	-1.2	3.5	2.0	-0.1	1.0	0.6

Values for the sum of squares due to linear trend for the shorter series of control trials, for each subject and each parameter. The weighting coefficients employed were +1 0 -1 for trials 1-3.

G_1 - G_4 as for table 8.

Table 9

SOURCE	D.F.	S.S.	S.S.	S.S.	
Within subjects (difference)	40	92.50	165.70	14.77	
T(difference)	1	0.11	6.96	1.15	
G x T(difference)	3	21.44	24.89	0.91	
O x T(difference)	1	5.51	0.004	0.002	a.
(G x O) x T(difference)	3	15.64	16.47	0.51	
Error x T(difference)	32	49.80	117.39	12.19	
Within subjects (difference)	40	74.50	65.15	12.47	
T(difference)	1	0.01	0.14	0.16	
G x T(difference)	3	2.34	1.66	0.94	
O x T(difference)	1	0.31	0.46	0.42	b.
(G x O) x T(difference)	3	3.44	7.34	0.08	
Error x T(difference)	32	68.40	55.50	10.87	

The components of the within subjects sums of squares that arise from the difference between the first experimental trial and the immediately preceding control trial, in order, for the number of alternations, the mean dominance time of the right field, and the mean dominance time of the left field. Analyses undertaken separately for the blocks of trials involving the longer (a) and shorter (b) series of successive control trials.

Code for symbols, as in table 7.

Table 10

Number of alternations

G_1	-4	-2	-3	-1	-6	3	-4	2	0	0
G_2	1	0	0	2	-1	-1	1	0	-3	-1
G_3	1	3	-1	0	3	0	0	5	-1	1
G_4	1	3	2	0	0	-1	0	1	3	0

Mean duration of dominance of right field

G_1	3.4	0.5	0.2	0.0	0.5	-2.5	0.3	-1.8	-0.6	-0.9
G_2	-0.6	-0.8	0.2	-0.9	1.4	0.9	-0.2	-0.2	2.0	0.7
G_3	-0.5	0.5	2.1	-0.2	-0.2	1.4	0.3	-1.4	-0.6	0.3
G_4	-2.2	-15.7	-5.4	1.2	-0.2	0.2	-0.3	0.0	-1.7	-1.0

Mean duration of dominance of left field

G_1	0.6	0.2	0.7	0.8	0.2	0.7	1.0	0.4	0.6	0.6
G_2	-0.2	0.8	-0.3	0.1	0.0	0.6	0.0	0.2	0.5	0.1
G_3	-0.5	0.5	2.1	-0.2	-2.0	1.4	0.3	-1.4	-0.6	0.3
G_4	0.2	0.4	0.4	-1.2	0.2	2.8	0.3	-0.5	-0.8	0.3

Values for the sum of squares due to the difference between the first experimental trial and immediately preceding control trial, for the block of trials involving the longer series of successive control trials, for each subject and each parameter. The weighting coefficients employed were +1 and -1 for the control and experimental trials respectively.

G_1 - G_4 as in table 8.

Table 11

Number of alternations

G_1	2	1	-3	2	2	-5	-2	3	-3	0
G_2	0	4	-2	0	1	-5	-1	0	1	-1
G_3	-2	1	2	-1	0	0	0	4	0	1
G_4	0	0	1	0	0	0	1	-1	1	0

Mean duration of dominance of right field

G_1	-2.2	0.3	0.4	-2.4	0.0	1.2	0.1	-1.6	5.6	-0.6
G_2	0.1	-0.7	-0.2	-0.2	-1.7	6.5	0.1	-0.6	-0.1	-0.4
G_3	-0.1	-0.5	-1.1	-0.3	0.0	-1.8	0.2	-0.2	-0.7	-0.3
G_4	0.2	-0.1	-1.9	0.0	-0.2	2.9	-4.4	1.0	-0.1	0.5

Mean duration of dominance of left field

G_1	-0.3	-0.8	0.4	0.5	-0.3	0.3	0.6	0.0	0.8	0.0
G_2	-0.1	-0.4	0.8	0.1	0.3	-0.5	0.2	0.6	-0.3	0.2
G_3	1.0	-0.2	-0.4	1.4	0.0	1.9	1.8	-1.7	0.1	-0.1
G_4	-0.3	0.4	0.9	0.0	0.2	-2.5	-0.7	0.2	-0.2	-0.3

Values for the sum of squares due to the difference between the first experimental trial and immediately preceding control trial, from the block of trials involving the shorter series of successive control trials, for each subject and each parameter. The weighting coefficients employed were +1 and -1 for the control and experimental trials respectively.

G_1 - G_4 as in table 8.

Table 12

SOURCE	D.F.	S.S.	S.S.	S.S.
Between subjects	39	5193.1	3450.9	1518.8
G	3	940.4	468.7	378.3
O	1	47.2	6.2	26.7
G x O	3	464.4	92.7	48.0
Between subjects within groups (Error)	32	3741.1	2883.3	1065.8
Within subjects	240	706.5	1871.7	181.5
T	6	22.0	34.5	4.7
T x G	18	99.3	79.7	16.9
T x O	6	16.2	22.9	4.6
T x (O x G)	18	72.4	294.9	8.9
T x Error	192	496.6	1439.7	146.3
Total	279	5899.6	5322.6	1700.3

Results of the analyses of variance on the data from the longer series of successive control trials, applied, in order, to the number of alternations, the mean dominance times for the right field and the mean dominance time for the left field.

Code for symbols as in table 7.

Table 13

SOURCE	D.F.	S.S.	S.S.	S.S.
Between subjects	39	2174.5	3345.8	310.2
G	3	656.2	874.6	107.5
O	1	19.2	214.4	7.8
G x O	3	27.3	383.0	10.4
Between subjects within groups (Error)	32	1471.8	1873.8	184.5
Within subjects	80	235.3	428.9	40.5
T	2	11.5	14.7	0.2
T x G	6	23.0	55.4	5.2
T x O	2	12.6	18.7	0.4
T x (O x G)	6	5.7	36.4	3.1
T x Error	64	182.5	303.7	31.6
Total	119	2409.8	3774.7	350.8

Results of the analyses of variance on the data from the shorter series of successive control trials, applied, in order, to the number of alternations, the mean dominance times for the right field, and the mean dominance time for the left field.

Code for symbols as in table 7.

Table 14

RESULTS AND ANALYSIS

No subject had to be rejected on the basis of the interrogation concerning the subliminal condition; that is, no subject reported being aware of the stimuli that were superimposed on the right field in the subliminal conditions.

Before proceeding with the detailed analysis, it will be useful to give a rather more specific interpretation to the hypothesis under test. To reiterate, it was predicted that:

(i) there would be evidence of habituation toward the control stimuli in the longer series of control trials. Moreover, since it necessarily involves some sort of response toward the stimuli in the first instance, habituation should occur in those conditions and involve those parameters as dictated by Levelt's thesis;

(ii) changes in the rivalry alternations in response to the meaningful content of the experimental stimuli would be dependent upon such prior habituation and, therefore, would be evident only following the longer series of control trials. These changes would also conform to the interpretation of Levelt's thesis, being restricted to the suppressed conditions and involving a reduction in the average duration of the suppressed phases of the right field and an increase in the number of alternations. No changes in the duration of the dominance phases of the right field would be anticipated;

(iii) the sensitivity toward the experimental stimuli when presented at a subliminal level would be more evident on the second of two successive trials involving such stimuli;

(iv) not unrelated to the first prediction, the control stimuli themselves would influence the rivalry alternations, again according to the interpretation of Levelt's thesis.

Illustrated in Fig 9 are the values, averaged across subjects, for the different parameters. The distinction according to the order in which the blocks of trials were undertaken is ignored in the figure.

(i) On the basis of the first prediction, it was anticipated that there would be evidence for a trend across successive control trials in the two suppressed conditions. To test this, for each parameter, the linear trend component was extracted from each of the Within Subjects sums of squares of the analysis of variance (cf. Table 7) (Winer, 1971). Presented in Tables 8 and 9 are the values for the sum of squares due to linear trend for each of the control series, for each subject and for each parameter. The only evidence for a significant linear trend involved the seven control trials in the suppressed/subliminal condition. As predicted, this habituation involved a reduction in the number of alternations across successive trials ($F = 7.735$; $df = 1,32$; $P < 0.025$), though this was not reflected in a significant increase in the mean duration of dominance of the left field. As anticipated, there were no significant changes in the mean duration of dominance of the right field.

(ii) In the same way that the sum of squares due to linear trend was extracted from each of the Within Subjects components, so the sum of squares due to the difference between the last control and first experimental trials was extracted in order to test this second prediction (cf Tables 10, 11 & 12). As predicted, though with one minor exception (cf below), the results conformed to the interpretation of Levelt's thesis. Moreover, the significant effects were confined to the condition in which there was evidence for habituation toward the control stimuli. Thus, only following the longer series of control trials in the suppressed/subliminal condition was there a significant difference between the first experimental trial and the preceding control trial. This difference reflected a significant increase in the number of alternations in response to the experimental stimulus, ($F = 7.23$; $df = 1,32$; $P < 0.025$) that was accompanied by a significant reduction in the mean duration of the suppressed phase of the right field ($F = 4.42$; $df = 1,32$; $P < 0.05$). Separating the subjects according to the order factor, the former effect was significant only for the group undertaking the longer series of control trials first, hence the significant T(difference) x (GxO) term in the ANOVAR (cf Table 10). As anticipated, there were no changes

in the mean duration of the dominance phases of the right field. Although the statistical analysis revealed a significant increase in the duration of the dominance phases of the right field following the longer series of control trials in the dominant/ supraliminal condition ($F = 8.59$; $df = 1,32$; $P < 0.025$) it was the extreme result from just one subject that appeared responsible for this. Thus, with just one subject's result omitted from the significant test, the F value dropped to 1.338 which is well below that required for significance at the 5% level.

(iii) To test this third prediction, the sum of squares due to the difference between the two experimental trials was extracted from each of the Within Subject components. There were no significant differences of this nature.

(iv) It would follow from the fourth prediction that, considering the control trials, overall differences in the rivalry alternations should appear between the subjects in the four different conditions of stimulus presentation. Though it weakens the analysis somewhat, in view of the fact that, in this and Experiment 1, there has been a consistent failure to detect any significant changes in the rivalry alternations in the dominant/ subliminal condition, this condition was adopted as a control against which the results of the other groups could be contrasted. The overall ANOVAR tables for the different parameters, as they relate to the control trials alone, are given in Table 13 & 14. Multiple comparisons assigned significance to a number of effects and showed that the results were consistent with the literal interpretation of Levelt's thesis. Thus, with just one relatively minor exception, the significant effects were restricted to the suppressed conditions, and to the number of alternations and the average duration for which the right field was suppressed. With reference first to the longer series of control trials, there were no significant differences between the two dominant conditions in terms of any of the three parameters. In contrast, there were significantly more alternations in both of the suppressed compared to dominant conditions ($F = 7.186$; $df = 1,32$; $P < 0.025$), (Note that this is a relatively weaker test of the original hypothesis than was initially intended.

Contrasting the two suppressed conditions individually with the dominant/subliminal condition just failed to yield significant results) and a significant reduction in the average duration of suppression of the right field when comparing both the suppressed/subliminal ($F = 7.55$; $df = 1,32$; $P < 0.025$) and suppressed/supraliminal ($F = 8.34$; $df = 1,32$; $P < 0.025$) conditions with the dominant/subliminal control condition. As anticipated, there were no comparable effects involving the average duration of dominance of the right field. With regard to the shorter series of control trials, there was again no difference between the two dominant conditions except that the average duration of dominance of the right field was significantly greater in the supraliminal condition ($F = 9.3$; $df = 1,32$; $P < 0.01$). In contrast, there were significantly more alternations in the two suppressed conditions when compared with the dominant/subliminal control condition ($F = 4.49$; $df = 1,32$; $P < 0.05$) and a significant reduction in the average duration of suppression of the right field when both the suppressed/subliminal ($F = 12.68$; $df = 1,32$; $P < 0.005$) and suppressed/supraliminal ($F = 14.5$; $df = 1,32$; $P < 0.005$) conditions were compared with the dominant/subliminal control condition. Again, as anticipated, there were no comparable differences involving the average duration of dominance of the right field. As in the case of the longer series of control trials, these effects, including the absence of any changes in the average duration of dominance of the right field, are entirely consistent with the literal interpretation of Levelt's thesis. It must be noted, however, that there was the one exception viz. the increased average duration of dominance of the right field in the shorter series of control trials in the dominant/supraliminal condition. Though it will be noted that a similar difference did not appear in the longer series of control trials, this anomalous result requires some consideration. Perhaps the first thing to note is that this result does not accord with Levelt's original thesis and, therefore, is most probably a result of some factor other than the increase in stimulus strength that is accorded the right field as a result of presenting the control stimuli. The most

likely possibility that suggests itself upon inspection of the individual subjects' results is that subjects in this condition responded to the presentation of the stimuli by developing right-eye dominance. This would be consistent with the fact that this anomalous effect only arose for those subjects who undertook the shorter series of control trials last. Because of this latter fact, together with its inconsistency with other aspects of the data and its nonconformity with Levelt's original thesis, this anomalous result should not detract too much from the other significant results.

This evidence, which supports the fourth prediction, is consistent with the appearance of habituation in the longer series of control trials in the suppressed/ subliminal condition, since both indicate that the control stimuli themselves were influencing rivalry, in accordance with the literal interpretation of Levelt's thesis. Moreover, since the changes in overall illumination that accompanied the presentation of subliminal control stimuli are unlikely to be responsible for these effects on rivalry (cf Levelt, 1966), support for this fourth prediction is also support for the hypothesis that the structural details of the suppressed stimulus are discriminated.

To summarize, the results confirm that the meaning of a stimulus may be discriminated when it is presented within the currently non-dominant field. The course of rivalry alternations is sensitive to the meaning of a rivalling stimulus in a manner that is consistent with the literal interpretation of Levelt's thesis. Thus, only when the stimulus was presented to the currently suppressed field were there any effects on rivalry, and these effects were confined to a reduction in the mean duration of suppression of the corresponding eye field and a consequent increase in the frequency of alternations. The more meaningful the stimulus residing in a suppressed field, the quicker this field recovers from the suppression. Again, these results were obtained with stimuli that were presented at a

subliminal level. Furthermore, the "meaningless" control stimuli themselves exerted comparable effects on the course of rivalry. Thus, when these stimuli were presented to the currently suppressed rather than the currently dominant eye field, the duration for which this field remained suppressed was reduced, though its duration of dominance was unaffected. Finally, confirming the suspicions aroused by the pilot study, these responses to the control stimuli habituated and it was only after this that the effects of the meaningfulness of the experimental stimuli emerged.

DISCUSSION

The results support the hypothesis that the meaning of a stimulus may be discriminated when it is presented within the currently non-dominant field in binocular rivalry. In addition to the direct support for this hypothesis the many different aspects of the data, with only minor failures to attain significance, support the theory that it is the currently non-dominant field in rivalry that takes precedence in determining the moment of alternation. Thus, in this, as in the movement study, the results confirm the literal interpretation of Levelt's thesis. In addition to these findings the suspicions aroused by the failure of the pilot study, concerning the possible need for habituation toward the control stimuli, were confirmed. Only in the condition in which there was habituation toward the control stimuli was there evidence for a response toward the meaningfulness of the experimental stimuli. The fact that habituation was only evident in the suppressed condition, and involved changes in those parameters as dictated by Levelt's thesis, adds further support to the literal interpretation of this thesis. Moreover, since this habituation could not have been to any structural detail per se (since this was changed on successive trials and equally so for the control and experimental trials) but rather to the general character of the control stimuli, it does in itself provide evidence that relatively abstract information may be derived from a suppressed and subliminal stimulus. In addition, it was confirmed that the mechanism that is capable of responding to non-dominant information in rivalry, is also capable of responding to subliminal material. Finally, it was not found that presenting a subliminal stimulus for a second time gave rise to a more significant response.

It remains to be understood why there was no change in the course of rivalry in response to the meaningfulness of the experimental stimuli following the longer series of control trials in the suppressed/supraliminal condition. Taken in conjunction with the lack of any sign of habituation in the control trials,

two possibilities suggest themselves. Firstly, it may simply be that the rivalry in this condition was insensitive to anything other than structural details. Secondly, the habituation may have been retarded, to the point of not emerging over the seven control trials, by the increased contrast of the supraliminal stimuli. Any response toward the meaningfulness of the experimental stimuli would thereby fail to reveal itself. Whilst the present data cannot distinguish between these two possibilities, which are not mutually exclusive, there is other evidence that is consistent with the first. Thus, it has been found that for the supraliminal, in contrast to the subliminal presentation of a stimulus, structure may be a more potent determinant of a subject's response toward the stimulus than its meaning (cf Dixon, 1972).

Finally, an alternative explanation of the results demands consideration. The critical difference between the experimental and control stimuli may relate to the familiarity of the structural information contained therein. It may be argued that the experimental stimuli involve much more familiar structures and that it is this, rather than the category of 'meaningful' stimuli to which they belong, that is responsible for the results. There are two objections to this alternative. In the first place, if we consider the fine structure of the control and experimental stimuli, then the manner in which the control stimuli were constructed ensured that in this respect the stimuli were similar. Secondly, the supposed effect of familiarity would contradict the findings with regard to the role of habituation, which indicates that it is the more unfamiliar stimulus that is best able to influence the course of binocular rivalry.

3.4 GENERAL DISCUSSION OF EXPERIMENTS 1, 2 & 3

In demonstrating that the non-dominant stimulus in rivalry is fully encoded, the results confirm the interpretation given in the studies reviewed in Chapter 2 and, bearing in mind the analogy with dichotic listening, they suggest that a theory in line with the Deutschs' treatment of selective attention is the more applicable to rivalry. Thus, more sophisticated parameters of a non-dominant stimulus may be encoded than Broadbent's (1958) model would allow. With regard to Triesman's (1969) model, it must be said that the meaningful stimuli employed in Experiment 3 were not chosen to be particularly significant for each subject. One would not expect that the internal units responsible for dealing with these stimuli would have lowered thresholds in the same way that the units responsible for signalling the presence of one's own name have. Moreover, that meaningfulness may be encoded even for a non-dominant stimulus that is otherwise subliminal indicates that any attenuation of non-attended material, if it does occur (Triesman, 1969), must be unsubstantial.

3.4.1 Tentative suggestions as to the neurophysiological structures mediating the response to the currently non-dominant information in rivalry:

It will be instructive at this stage to briefly reconsider he findings of the preceding experiments and to offer some broader-based, though tentative, theoretical analysis in the light of recent neurophysiological data. These data, it will be argued, suggest that visual centres in the midbrain and related association cortex are likely candidates for the mediating structures in the response to the currently non-dominant information in rivalry.

Experiments 1 and 2 demonstrated that movement may be discriminated under conditions that prevent the subject from being aware of the stimulus. A study that has been reported since these experiments were completed confirms this finding and, in addition, suggests a mediating role for midbrain structures. Poppel, Held

and Frost (1973) observed an increase in the amplitude of a patient's saccadic eye movements which was correlated with the eccentricity of a moving target that was presented within the 'cortically' blind area of his visual field. Because of the presence of the striate lesion, the patient remained totally unaware of the moving stimulus.

Bearing in mind the parallel that has been drawn between the perceptual suppression in binocular rivalry and that occurring in strabismus amblyopia, a recently-proposed theory of the deficit associated with strabismus (Ikeda and Wright, 1974) implicates the midbrain in the observation that a non-dominant stimulus may be discriminated. Ikeda and Wright propose that whilst the principal pathway from the amblyopic (suppressed) eye to striate cortex, via the lateral geniculate nucleus, is non-functional, the parallel retino-superior colliculus pathway is able to function normally. (Supporting this theory, Weiskrantz (1972) has recently described the visual capacity of destriate monkeys as amblyopic (cf below)). With reference to Experiment 2, their own and other research has implicated the latter pathway in the discrimination of movement (eg Ikeda and Wright, 1972; Horn and Hill, 1966; McIlwain and Buser, 1967).

With respect to the finding that the discrimination of a stimulus within a non-dominant field is possible even for a stimulus that is otherwise subliminal, again the superior colliculus-association cortex complex may be implicated. Focusing on the discrimination of movement it is the case, as Ikeda and Wright demonstrate, that cells comprising the pathway to the superior colliculus are particularly sensitive to moving stimuli. Therefore, compared with cells comprising the principal pathway terminating in striate cortex, they are the more capable of responding to a moving stimulus of low contrast (Ikeda and Wright, 1972). Similarly, Bender (1973) has observed that pattern discrimination in monkeys with inferotemporal lesions (the area of cortex to which superior colliculus projects) is particularly disrupted at low levels of illumination, suggesting that under such conditions the geniculo-

striate system is not the dominant visual system. Moreover, as will be discussed below, it is the case that the superior colliculus and association cortex, when functioning independently of primary visual cortex, do so without a perceptual adjunct to the information with which they are dealing.

Concentrating on Experiment 3, two features of the results are consistent with the hypothesis that the observed sensitivity toward information in the non-dominant field is mediated by this second visual system, and not by the geniculo-striate system. Firstly, with reference to the meaning of the non-dominant stimulus, there is evidence that the superior colliculus-posterior association cortex system is sensitive to the rather complex parameters of a stimulus, such as its meaning or significance, which contrasts sharply with the geniculo-striate system (cf Begleiter et al 1967, 1969; John et al 1967; Gross, 1973). Secondly, with reference to the observed habituation toward the non-dominant stimulus, both superior colliculus and related association cortex, again in contrast with the geniculo-striate complex, are known to be sensitive to novelty and hence susceptible to habituation (Walter, 1964b, 1965; Buser and Bignall, 1967; Thompson et al 1969, 1970; Horn and Hill, 1966; Brazier, 1964; Pagni, 1967).

These different aspects of the data are consistent then with the notion that it is the midbrain-association cortex that is responsible for the response to the currently non-dominant information in rivalry. Moreover, this notion accords with the literal interpretation of Levelt's thesis, but, before this is considered, it must be asked whether this second visual system plays anything other than a very minor role in vision, particularly when striate lesions are known to cause complete blindness in man (Kluver, 1942), and whether what is understood of its function is consistent with its role in rivalry. It will be argued that the superior colliculus-association cortex system and the geniculo-striate system have complementary functions in vision and selective attention, and that this is consistent with their proposed contribution to rivalry and with the literal interpretation of

Levelt's thesis.

A number of researchers have distinguished two modes of visual processing and have identified these with the midbrain and geniculo-striate systems.

Studying form discrimination in fish, Ingle (1967) discovered that their responses to direction in a stimulus depends upon whether the stimulus is processed by an orientating or a shape-analyzing system, which he characterizes as "Look" and "OK..eat" systems respectively. Held (1968) argued that whilst a spatial orientational visual system in higher mammals is perfected during interaction with the environment, (response produced visual feed-back being the critical factor) and is capable of modification with the prismatic distortion of vision, a pattern-analyzing system displays much less plasticity. Thus, Held points out that the deficiency in vision that results from rearing kittens in a pattern-less environment is not revealed by a testing procedure that does not call upon the animals orientating ability. Similarly, Schneider (1967 , 1969) has shown a high dgree of dissociation between two aspects of vision, visual localization and visual discrømination, as a result of comparing the effects of ablating either the colliculus or visual cortex in hamsters. After ablation of visual cortex hamsters discriminated the identities of visual patterns poorly but showed nearly normal ability to localize the same patterns by means of vision. Ablation of the superior colliculus produced just the opposite effects. Finally, Trevarthen (1968) has shown that what seem to be the same aspects of vision may be dissociated in split-brain monkeys, and has labelled them "ambient" and "focal" vision. Again these are associated with the midbrain and geniculo-striate systems respectively and, arguing that visual perception and action are intimately bound together, Trevarthen emphasizes that the distinction between these two systems must carry through to define two kinds of action or movement:

> "There are, indeed, two main kinds of acts made in the behavioural space, and each has its own dependency upon visual afference for guidance and confirmation. Orientations of the head, postural adjustments, locomotor displacements change the

relationship between the body and spatial configurations of contours, surfaces, events, and objects. These movements occur within what I shall call ambient vision. In contrast, praxic actions on the environment to use pieces of it in specific ways are performed with the motor apparatus of the body and the visual receptors oriented together so that both vision and the acts inflicted on the environment occur in one part of the behavioural space. The vision applied to one place and a specific kind of object, or deployed in a field of identified objects, I shall call focal vision. It is this examining and identifying kind of vision, serving refined and discriminating acts, which has evolved to quite a new level of proficiency and complexity in primates, especially man"(p 32).

Suggesting that two relatively distinct visual systems each make a significant contribution to vision in man is the residual visual capacity that survives geniculo-striate lesions. Recent observations have revealed a considerable residual visual capacity in monkeys after occipital ablation (Humphrey and Wiśeskrantz, 1967; Wiśeskrantz, 1972; Schilder, Pasik and Pasik, 1972; Humphrey, 1974). Thus, if tested under the appropriate conditions, these animals are capable of (i) differentiating figure from ground, (ii) locating figures/objects in space sufficiently well for eyes, head and hands to be directed towards them, (iii) moving swiftly around in an environment full of objects, and finally (iv) retrieving small pieces of food or paper from the floor (cf Humphrey, 1974). Discussing the surprising visual capacity of destriated monkeys, Wiśeskrantz (1972) concludes that their vision is no worse than amblyopic, being the equivalent of normal peripheral vision over the entire field. Humphrey (1974) concludes that the visual capacity of his destriate monkey eight years after the operation is best described as a permanent loss of 'focal' vision, with 'ambient' vision remaining intact. Apart from anything else this provides strong support for Trevarthen's theoretical analysis.

Recent experiments on human subjects have revealed a similar visual capacity that is able to survive occipital lesions. A number of experiments have supported an early study (Bender and Krieger, 1951) in which it was observed that patients with unilateral geniculo-striate lesions were able to respond to visual stimuli presented within the 'blind' part of their visual field and, more specifically, were able to point by hand at these stimuli.

Richards (1973) has shown that patients are capable of responding to depth information when this is presented within a cortically-blind area of the visual field, even though they report seeing nothing. Poppel, Held and Frost (1973) demonstrated that when moving stimuli are presented within a patient's blind field, the amplitude of voluntary saccades toward the unseen stimuli increases for more eccentric targets. Sanders et al (1974) have demonstrated, in a patient with a restricted lesion of the right occipital lobe, a surprising visual capacity. Their patient was able to shift his fixation toward the location where a stimulus had been presented in his blind field, point to the same location with his forefinger, 'guess' correctly whether a stimulus that had been presented was a vertical or horizontal line or whether it was an 'X' or 'O', and 'guess' whether a sine wave grating had been presented. Indeed, by varying the spatial frequency of the grating in the latter condition, it was found that the corresponding acuity threshold was 1.85' for the scotoma, as compared with 1.49' for the symmetric region in the intact field. Finally, Perenin and Jennerod (1975) have confirmed that patients with post-geniculate lesions are able to accurately point at the origin of a stimulus presented within the blind area of the visual field. Unlike Sanders et al, however, these authors were unable to show any capacity in the patients to respond to the 'shape' of the unseen stimulus.

Is there any evidence that the midbrain-association cortex contributes significantly to this residual visual ability? Most of the evidence is indirect, particularly for the human studies, though researchers have suggested, by a process of elimination and with varying degrees of conviction, that it is these structures which are responsible for the residual capacity in their patients.

We have seen that Humphrey (1974) concluded that the destriated monkey retained the capacity for ambient vision and, in view of Trevarthen's analysis, this implicates the midbrain system in its residual visual capacity. Pointing in the same direction is Wieskrantz's (1972) conclusion that the destriate monkey is effectively amblyopic. Thus, Schneider (1969) has suggested that

the amblyopic eye of humans yields a type of vision that is comparable to that observed in destriate animals. Similarly, as has already been mentioned, Ikeda and Wright (1974) have recently proposed that the various forms of amblyopia result from the failure to activate sustained neurones during development and that, therefore, amblyopic vision reflects the functioning of transient neurones, which comprise the principal pathway to the superior colliculus in cats (Ikeda and Wright, 1972). Consistent with this, the (transient) neurones transmitting to the superior colliculus may be distinguished from those (sustained) neurones primarily comprising the geniculo-striate system on the basis that their receptive fields are relatively more evenly distributed over the whole visual field. It will be remembered that amblyopia is the equivalent of normal peripheral vision over the entire visual field. In conclusion, the amblyopic nature of the destriated monkey's vision is consistent with the notion that it is mediated by the midbrain-posterior association cortex system.

Finally, direct evidence on the structures mediating the residual visual capacity of the destriate animal is given mention by Weiskrantz (1972), who reports that "the information that is being exploited in the totally-destriated brain is almost certainly received by, and is processed by, the posterior association (infero-temporal) cortex, because if this area is also removed all but very crude discriminations seem to be impossible". Denny-Brown and Chambers (1955) have also reported that the residual visual capacity that survives striate lesions is abolished by lesions to this cortical region.

To summarize, this evidence for the existence of two visual systems which may be identified with the midbrain-association cortex and geniculo-striate systems, indicates that the former makes a significant contribution to vision, even in man. It may next be asked, therefore, whether the function of the former system is consistent with its proposed involvement in binocular rivalry.

The studies of Ingle (1967), Held (1968), Schneider (1967, 1969) and Trevarthen (1968) are consistent in suggesting that the midbrain

system is responsible for orienting behaviour. Supporting this, Denny-Brown (1962) observed that a monkey with both superior colliculi removed shows no orientation to visual events even though the projection to visual cortex is intact. Some recent neurophysiological data at the single-cell level support this:

In their micro-electrode studies Ikeda and Wright (1972) (cf also Cleland, Dubin and Levick, 1971) found that the following properties distinguished transient from sustained neurones: (i) Relatively more likely to have receptive fields in the peripheral visual field; (ii) Respond poorly to high spatial frequencies (cf Schiller and Koerner (1971) below; (iii) Are particularly sensitive to movement and change, displaying a high degree of temporal resolution; (iv) Possess fast conducting axons. On the basis of these and additional characteristics of transient neurones, Ikeda and Wright suggested that "the input to the brain from transient cells is concerned with the organization of fixation reflexes and orientation responses which have the effect of bringing an object of interest into sharp focus on the fovea, where sustained cells take over the task of accurate registration of spatial characteristics of the stimulus" (1972, p 796). It will be remembered that the principal terminal site for transient neurons is the superior colliculus, and for sustained neurons the lateral geniculate (Ikeda and Wright, 1972). That the superior colliculus is involved in eye movements is revealed by a number of other studies. For example, Schiller and Koerner (1971) found that single units in the superior colliculus of a wake monkey respond to provocative stimuli such as moving and flashing lights, but are very poorly tuned to shape or direction of movement. More importantly, some of the units discharged in advance of a rapid eye movement of a particular size and direction and the receptive fields of these units tended to lie in just the target area to which the fovea was directed by the eye movement. Wurtz and Goldberg (1972) have demonstrated, however, that the superior colliculus in monkey is not simply involved in providing the target information for the accurate guidance of eye movements (as is traditionally thought) but rather contributes to the shifting of attention by selectively facilitating

the appropriate eye movements.

That the superior colliculus is involved in shifting attention (orienting) and, ipso facto, is capable of responding to information that is not currently at the focus of attention, is supported by other data, and indeed, is consistent with its supposed role in binocular rivalry. This change of emphasis from the orienting response to shifts in attention (the critical difference being that overt movements need not accompany the latter) becomes appropriate when the effects of lesions in posterior association cortex are considered. These effects confirm that the midbrain-posterior association cortex is involved in shifting attention and, ipso facto, is capable of responding to information that is not currently at the focus of attention. This is consistent with the proposed contribution of this system to binocular rivalry.

In the Tree Shrew, whilst the lateral geniculate projects to striate cortex, the superior colliculus (via pulvinar) projects to the temporal, or extrastriate cortex. By comparing the effects of lesions in these different cortical regions, Killackey and Diamond (1971) have suggested that these two visual systems mediate reciprocal aspects of selective visual attention. Whilst the striate region participates in processes that enable attention to be focused and sustained on the relevant cue(s), the temporal region contributes to processes that induce a shift of attention from one cue (colour) to another (line orientation) when this is made relevant to successful performance. Killackey, Wilson and Diamond (1972) trained tree shrews to chose between two stimuli on the basis of the orientation of stripes and not on the difference in hue that was also present. When criterion performance was reached, hue became the relevant dimension and such shifts between hue and orientation continued. It was found that animals with temporal lesions were retarded in the initial learning of the problem but, more importantly, they reverted to chance level performance with each shift. Consistent with Schneider's results with hamsters, shrews with striate lesions failed to reach criterion in the initial problem. Describing the

critical effects of temporal cortex lesion in this instance, Killackey et al state that it 'produces an impairment in learning to shift attention from a previously-relevant dimension to a previously-irrelevant dimension'. These and other studies, therefore, extend the earlier notions of the function of the superior colliculus by suggesting that, in conjunction with related cortical regions, this system is also involved in shifting attention between the different aspects of the same stimulus, i.e, independently of any of the overt components of the orienting response.

With regard to studies of cat, although Gross (1973) doubts that the supralsylvian gyrus in cat is analogous to the inferotemporal cortex of monkey, it is the case that this area receives a direct projection from the pulvinar (lateral posterior nucleus of the thalamus) (cf Dow and Dubner, 1969 for references). One reason for his doubts was the fact that suprasylvian gyrus also receives a projection from the lateral geniculate body. However, the aspect of the lateral geniculate that projects to suprasylvian gyrus does so via the pulvinar and, moreover, does not project to striate cortex (Chalupa, Anchel and Lindsley, 1973).

Dow and Dubner (1969) employed a variety of moving and stationary stimuli to study the receptive fields of cells in a particular area of the suprasylvian gyrus of cat. They also attempted to assess how dependent these response-characteristics were upon primary visual pathways, and how much they reflected the responses observed in other regions of the brain. In respect of their receptive field size, the apparent lack of inhibitory surround and the phasic nature of the responses to stimulus onset and offset, Dow and Dubner commented that there was a remarkable resemblance to cells of the superior colliculus and not to cells of the geniculo-striate system. One exception proved to be layer B in the lateral geniculate but this layer projects, like superior colliculus, to the suprasylvian gyrus (via pulvinar) rather than to striate cortex (cf Chalupa, Anchel and Lindsley, 1973). In view of the response properties of cells in this posterior association cortex of the cat, Dow and Dubner concluded that this area is more likely to be involved in visual attention and orientation than in pattern discrimination, being

particularly sensitive to changes in stimulus parameters. Consistent with this, Thompson and Bettinger (1970) have suggested that the suprasylvian gyrus mediates an 'observing reaction'. They point out that neurons in this area are particularly susceptible to habituation, responding best to novel stimuli. Thus, they demonstrate that the evoked potential recorded over this area to a repetitive stimulus is markedly reduced in the presence of a novel or 'interesting' stimulus. Furthermore, close inspection of the properties of some individual cells indicated that they coded novelty in terms of both stimulus quality and recency. On the basis of their properties, Thompson, Bettinger, Birch, Groves and Mayers (1969) suggest that the cells in this association area function as Sokolov's (1960) hypothetical novelty cells.

In monkey, the lateral geniculate projects exclusively to striate cortex, and the superior colliculus, via pulvinar, projects to inferotemporal cortex and not to striate cortex (Gross, 1973). Whilst the effects of lesions in inferotemporal cortex appear to be more complex than those resulting from extrastriate lesions in the tree shrew, they bear a basic similarity to the latter and with the data from cat. Butter (1968) discovered that monkeys with inferotemporal lesions sampled, or attended to, fewer of the features in a display. In equivalence-testing following discrimination learning, they behaved as though they had utilized only one aspect of the patterns and not the whole form. Comparable results were obtained by Butter and Hirtzel (1970) in a problem involving different cues that were spatially separated. Thus, animals were trained to discriminate between compound stimuli which differed in brightness near the response site (manipulandum) and in hue more distant from the response site. In subsequent discrimination testing where only the distant cue was available, inferotemporal monkeys made significantly the most errors. Inferotemporal lesions would seem to have impaired the animal's capacity to respond to cues outside the focus of attention. Oscar-Berman, Heywood and Gross (1971) have shown that monkeys with inferotemporal lesions have altered patterns of eye movements during visual discrimination learning, shifting their gaze between the discriminanda much less frequently than normal monkeys. Bagshaw, Mackworth, and Pribram (1972) argue that

inferotemporal cortex is involved in directing attention to the relevant features of a stimulus, and Wilson, Kaufman, Zieler and Lieb (1973) have distinguished two areas within inferotemporal cortex, and have suggested that whereas one is concerned with directing attention on the basis of spatial information, the other is concerned with directing attention on the basis of time. Finally, Gerbrandt, Spinelli and Pribram (1970) have demonstrated that stimulation of inferotemporal cortex induces a state within striate cortex that is comparable to that which exists whilst the monkey is visually attentive.

To summarize, the evidence supports the notion that the superior colliculus-association cortex complex does make a significant contribution to vision, even in man. Moreover, the function that seems to be served by this complex is consistent with the rivalry data. It has been argued that this complex is responsible for initiating a shift in attention and, more generally, for orienting behaviour. Important for the present thesis, however, is the fact that, in line with this responsibility, this complex is particularly sensitive to information that is not currently being attended to. Clearly, this is a pre-requisite for any system that is to be responsible for initiating a shift in attention unless these are to be randomly distributed. This complex, then, appears to be involved in responding to, or 'noticing', new and unexpected stimulation, and its sensitivity to movement, novelty/habituation, low contrast (blurred) images, and to information in the peripheral visual field, are all consistent with the notion that it is responsible for responding to such attention-getting information (Ikeda and Wright, 1972; 1974). All this contrasts with the geniculo-striate system, which appears to be concerned with information toward which attention is currently being focused and sustained.

To conclude the general discussion of the results of Experiments 1 and 3, the rather paradoxical finding that the non-dominant stimulus in rivalry is not only capable of influencing the perceptual alternation process but actually takes precedence in this, is consistent with the proposed involvement of the second visual system. This confirmation of the literal interpretation of

Levelt's thesis suggests a dual nature to the visual system. Thus, whilst the one aspect is to be most intimately associated with the currently-dominant (attended) stimulus, the other is to be more associated with the non-dominant (unattended) stimulus, and with the rivalry alternations. The relatively independent functioning of the retino-geniculo-striate cortex and retino-superior colliculus-temporal cortex pathways (Gross, 1972; Killackey et al, 1972; Snyder and Diamond, 1968) fulfils these respective requirements. Thus, we have seen that whilst the former has been assigned a mediating role in the focusing or sustaining of attention (Killackey et al, 1972), the latter has been implicated in the assessment of the significance of a stimulus and in re-directing or shifting attention (Butter and Hirtzel, 1970; Gerbrandt et al, 1970; Gross, 1973; Pribram, 1971; Wilson et al, 1972). Very important for the present thesis is the fact, revealed in the clinical studies, that the midbrain-association cortex complex functions without a perceptual (phenomenal) adjunct to the information with which it is dealing. This is important for any system that is to be responsible for the visual system's responsiveness to currently-suppressed information in binocular rivalry.

This theoretical analysis of the neurophysiological data relating to two visual systems provides a context against which the evoked potential study that is reported below may be considered. The aim of this study was to confirm that a non-dominant stimulus is nevertheless discriminated by higher centres in the visual system, and to reveal more directly something of the physiological processes underlying rivalry. It will be seen that the findings of this experiment confirm and extend this theoretical analysis.

3.5 CRITICAL REVIEW OF THE LITERATURE RELATING DIRECTLY TO THE PHYSIOLOGICAL BASES OF BINOCULAR RIVALRY

3.5.1 Introduction

The 'Passive' and 'active' approaches toward perception, briefly outlined in Chapter 1, have rather different implications for the physiological processes underlying binocular rivalry. The first approach, it will be remembered, is based on the premise that there can be no analysis and hence no recognition, of a stimulus that goes unperceived (suppressed). Thus, according to this approach, in binocular rivalry there is either a direct competition between the two monocular channels such that the currently-dominant input prevents the contralateral information from being recognized, or some mechanism placed more centrally than the recognition machinery feeds back on to the contralateral channel. These two alternatives are illustrated in Fig 10a. The second approach, which holds that perception reflects active processes, does not work on the premise that there can be no recognition of a stimulus that goes unperceived and, therefore, does not demand that the non-dominant information in rivalry be prevented from attaining recognition; rather, it may be suggested, for example, that the contralateral information simply fails to contribute to a matching process that is the presumed correlate of perceptual experience. This alternative is indicated in Fig 10b, where 'pathway' 3 reflects the matching process.

If the visual cortex is identified as the structure primarily responsible for the recognition of visual stimuli, the two approaches may be given more specific interpretation. Whereas the first must predict that cortical involvement with respect to the recognition of the non-dominant stimulus is precluded, the second makes no such demand; rather it simply holds that the dominance of a stimulus will be reflected in those physiological processes that are involved in the matching function.

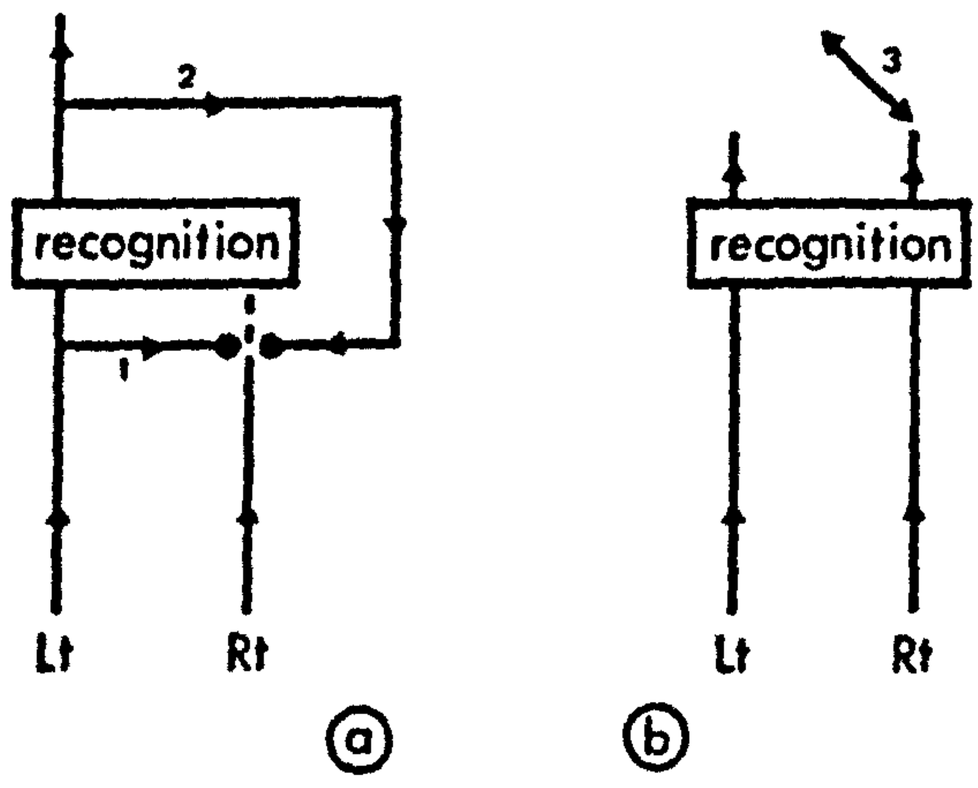
There are a number of neural pathways that could serve the purposes demanded by these different approaches. These are

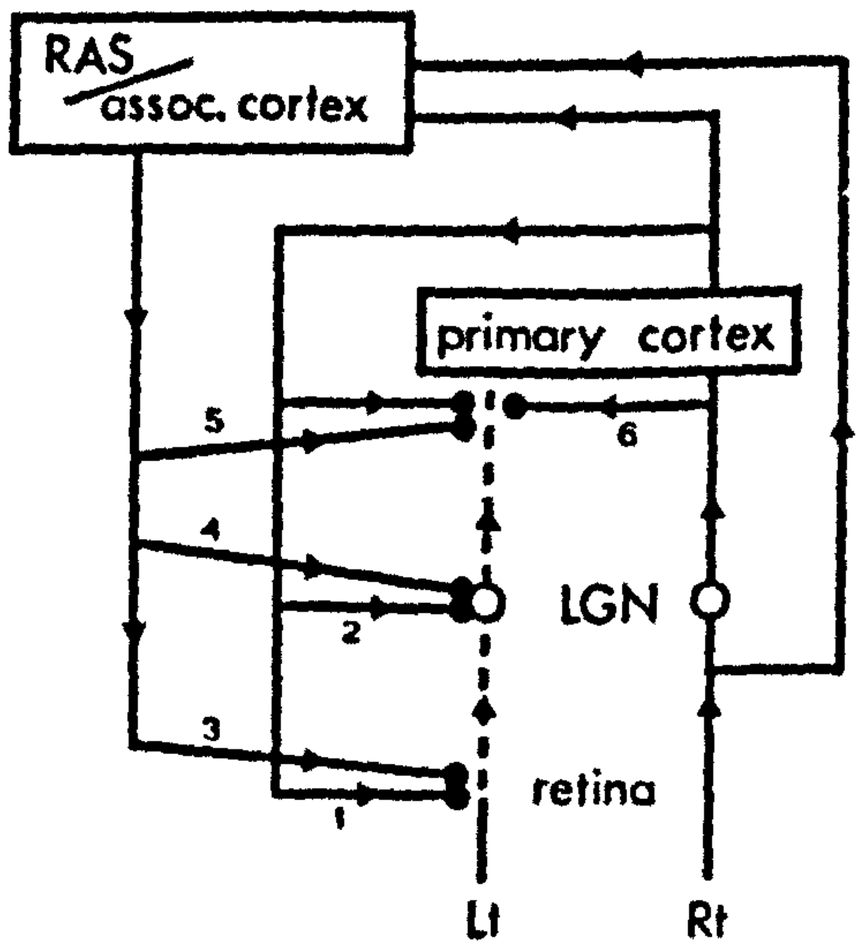
Figure 10 a,b

Schematic representation of the fundamental implications of the passive (a) and active (b) approaches toward perception for the information processing involved in binocular rivalry.

Figure 11

Neural pathways, known to exist, which would serve the various functions demanded by the passive and active approaches toward rivalry.


2
recognition
1
Lt
Rt
a
3
recognition
Lt
Rt
b


RAS
assoc. cortex
primary cortex
5
6
4
LGN
2
3
retina
1
Lt
Rt

illustrated in Fig 11. Pathways 1 and 2 represent two alternatives for the gating or attenuation of monocular information by efferents from within the visual system. Evidence for pathway 1 is provided by Dodt (1956) and for pathway 2 by Ogden (1960) and Mescherski (1966). Pathways 3 - 5 represent various alternatives for the gating of monocular information by efferents arising in structures outside the visual system, eg the reticular activating system or posterior association cortex. Evidence for the existence of such pathways, that terminate at a peripheral level, is provided by Hernandez-Peon, Scherrer and Velasco (1956) and Guerrero-Figueroa, Guerrero-Figueroa, and Heath (1964). Evidence for pathway 4 is again provided by Hernandez-Peon, Scherrer and Velasco (1956) and by Lindsley (1958), Spinelli, Pribram and Weingarten (1965) and Spinelli and Weingarten (1966). Auerbach, Beller, Henkes and Goldhaber (1961) have added yet another alternative. Arguing indirectly from their discovery that the b-wave of the ERG is smaller in binocular than monocular stimulation, Auerbach et al suggest that there exists a mutual inhibition of the two monocular systems through centrifugal fibres having a subcortical origin. With regard to the channel that is labelled 6 in Fig 11, there are two possibilities that have been suggested. First, Bishop (1973) and Jung (1961) have suggested that rivalry reflects the suppression of activity originating in one eye when the two inputs converge on a potentially-binocularly-driven cell in striate cortex. It is correctly assumed that the preference of a cell for a specific stimulus prevents it from responding to both of the stimuli in binocular rivalry. Second, Ratcliff (1962) suggested that lateral inhibition between cortical neurones receiving their information from different eyes, may be responsible for rivalry suppression. Finally, there is evidence that visual cortex and other cortical areas interact in a manner that could be the basis of the post-recognition processes upon which the second, active approach toward rivalry is based (cf Gross, 1973).

Whilst there are many possible contributors to the EEG other than activity in underlying cortex (cf Vaughan, 1969; Regan, 1973), evoked cortical potentials may be recorded that reliably reflect this activity (Cooper et al, 1965; Heath and Galbraith, 1966; Vaughan,

1969b; Vaughan & Ritter, 1970; Corletto et al, 1967; Thompson and Bettinger, 1970; Fromm and Bond, 1967; Minke and Auerbach, 1972). The evoked potential, therefore, suggests itself as a means of discriminating between the two approaches toward rivalry. Whilst the first approach would not allow for the existence of a cortically evoked potential to a stimulus that is temporarily non-dominant, the second, active approach, could accommodate this. It will be pertinent, therefore, to enquire as to the nature of the physiological indices that correlate with the perceptual effects of dichoptic interaction. Though perhaps only implicitly, the studies that are to be reviewed have considered the significance of the evoked potential in terms of the general notions introduced above.

3.5.2 Experiments demonstrating a form of dichoptic interaction that is reflected in the EEG but which is unlikely to be involved in binocular rivalry

Lansing (1964) purports to have demonstrated a correlation between the amplitude of the rhythmic EEG response to the flicker stimulation of one eye (recorded from electrode sites over midline occipital-parietal cortex) and the perceptual dominance of that eye in a dichoptic viewing situation. He presented a series of diagonal stripes illuminated by red light to a subject's right eye, whilst stimulating his left eye with a homogeneous, intermittently-illuminated field. It was observed that (i) increasing the intensity of the right field caused an overall decrease in the perceptual dominance of the flickering field, together with a reduction in the amplitude of the EEG response, (ii) the perceptual dominance of the right field could be reinstated by an abrupt change in its overall luminance level, and that this was accompanied by a reduction in the amplitude of the EEG response, and (iii) the spontaneous fading of the structured target was accompanied by an increase in the amplitude of the cortical response. The study, however, has three rather basic weaknesses. First, and with respect to the first condition, the possibility was not eliminated that in itself the presentation and variation of the contoured target caused the changes in evoked potential amplitude. This is particularly serious since the variation of luminance level was confounded with changes in contrast. A number of authors have provided data that would support this alternative explanation (cf. the work of Lehmann et al below). Second, except for the last condition Lansing's correlation is rather weak since it is between the <u>percentage of time</u> for which the left eye was judged dominant and the <u>overall</u> mean amplitude of the EEG response during the same period. There was no attempt to correlate individual periods of dominance and suppression with the EEG. Third, by stimulating at the alpha frequency, Lansing was especially prone to confuse changes in the evoked potential with changes in alpha abundance for two reasons. Thus, in the second condition the abrupt changes in luminance level themselves might be expected to bring about a desynchronization of the EEG (eliminating

or reducing alpha), and with respect to the third condition, Lehmann, Beeler and Fender (1965) have observed a correlation between periods of alpha abundance and the degeneration of an image.

Cobb et al (1976a), in an intended replication of Lansing's second condition, failed to confirm the change in amplitude of the evoked response to flicker with the illumination of the contra-lateral field. However, though it is unclear just what stimuli Cobb et al employed, it is the case that their condition deviated from Lansing's. Thus, in their study, either both fields were homogeneous or the field containing the structural information was intermittently illuminated, rather than the homogeneous field.

More satisfactory experiments belonging to this category were undertaken by Lehmann et al. As did Lansing, these workers observed the rhythmic EEG response to an intermittently-illuminated homogeneous field under various conditions of stimulation of the contralateral eye.

Lehmann, Beeler and Fender (1967) presented a flickering (3.2/sec) homogeneous field (circular and subtending 17 deg) to one eye, and a cross-shaped translucent target to the contralateral eye. The latter target was either presented normally or as a stabilized image. The authors observed (i) that the averaged potentials to the flickering stimulus were reduced in amplitude when the contralateral eye viewed a steadily-illuminated target instead of a blank field, and (ii) that this reduction was greater for the unstabilized image. Lehmann and Fender (1967) went further and compared the effects of presenting to the contralateral eye a black dot, cross and a grid of seventeen equally-spaced lines along each axis. They were able to demonstrate a direct relationship between the 'amount of structure' and the extent to which the evoked potential to the flickering field was reduced.

Finally, employing a slightly different set-up, viz. intermittently illuminating a structured rather than a homogeneous field, Riggs and Whittle (1967) have observed similar changes in the rhythmic EEG response as a result of stimulating the contralateral eye.

They observed that the amplitude of the response to the intermittent illumination of a field containing 19 parallel black and white diagonal lines was reduced when the contralateral eye viewed a continuously-illuminated grating oriented at right angles to the first.

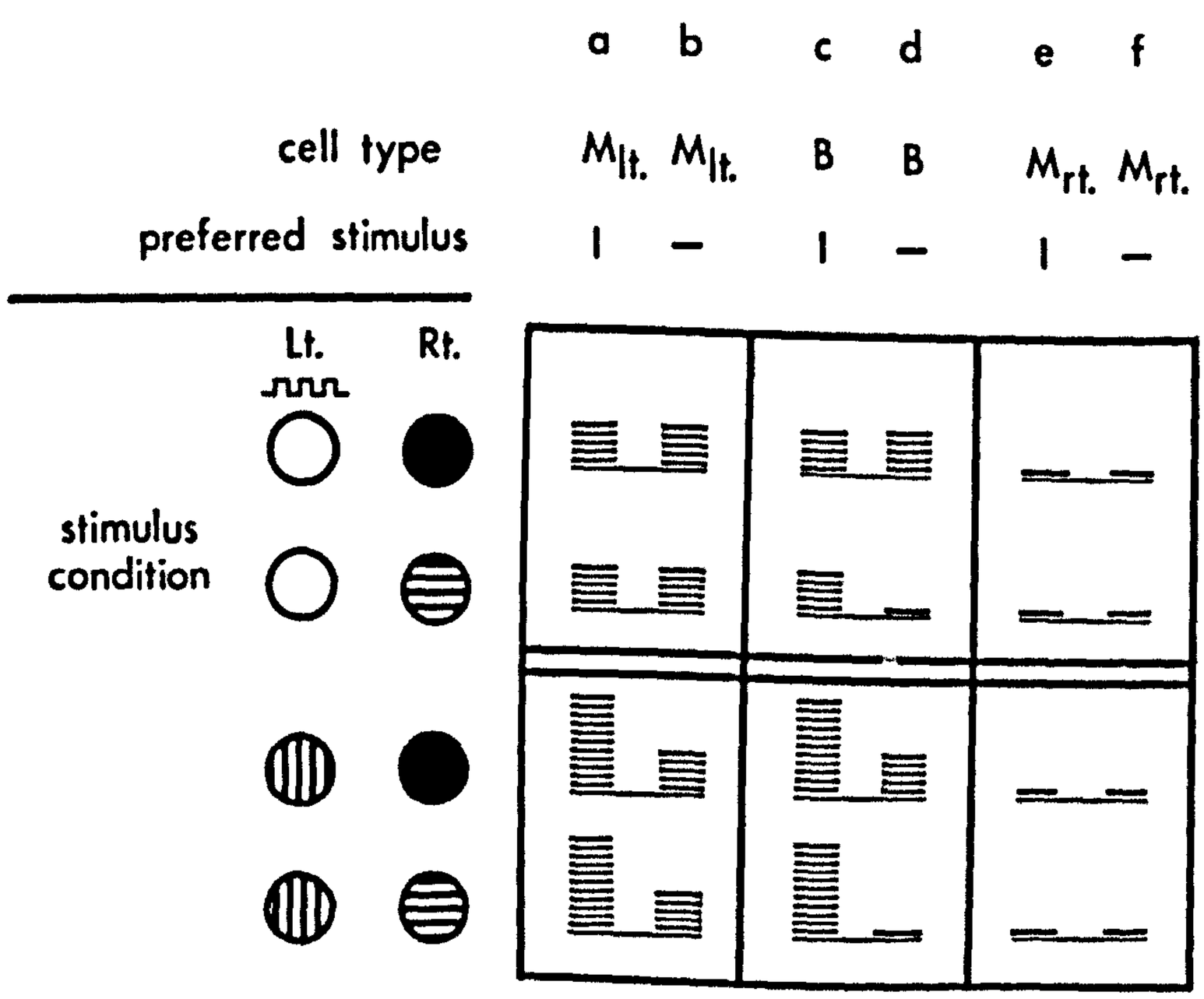
To summarize, these first studies demonstrate a form of dichoptic interaction that is reflected in the EEG. For two reasons, however, this interaction is unlikely to reflect a reversible inhibitory process of a kind that may underlie the phenomenal suppression that occurs in binocular rivalry.

First, though little attention was paid in these studies to a subject's perceptual experience, it would appear that despite the changes in amplitude of the evoked potential, the perception or sensation of 'flicker' remained. Lansing, in discussing the results from the third condition in his experiment, admits that his subjects found the spontaneous shifts in dominance difficult to judge because the dominance of one eye field over the other was "not great". Similarly, Riggs and Whittle (1967) indicated that a sensation of 'flicker' did remain in their dichoptic viewing conditions. Second, if we consider the behaviour of the visual system at the single-cell level, a rather different explanation of the interaction suggests itself. Schematically illustrated in Fig 12 is a sample of the wide variety of cells that we may assume reside in the human visual cortex (cf Marg, 1973; Kulikowski and King-Smith, 1973). M(l) and M(r) represent cells which respond exclusively to information originating in the left and right eye respectively (ie. monocularly-driven). Two of these cells respond optimally to a vertically-oriented edge, two respond optimally to a horizontally-oriented edge. Included are two binocularly-driven cells, B, having different 'preferred' stimulus orientations.

The rows in the figure represent the different stimulating conditions that have been employed in the above studies. The first two rows represent the experiments of Lehmann et al (1965; 1967a, b), whilst the third and fourth represent the conditions employed by

Figure 12

Schematic illustration of the behaviour of a sample of neurones from visual cortex during dichoptic stimulation of the kind employed in the first group of studies. The scheme offers an alternative explanation of the observed changes in EEG, an explanation that does not incorporate the notion of a reversible inhibitory process between the two monocular channels.


a b c d e f
cell type
$M_{lt.}$ $M_{lt.}$ B B $M_{rt.}$ $M_{rt.}$
preferred stimulus
Lt.
Rt.
stimulus condition

Riggs and Whittle (1967). For each cell and stimulating condition a 'bar' is shown whose height takes on one of three possible values depending upon whether the firing rate of the cell would be near maximum, at a resting level, or at some intermediate level.

Three assumptions are adopted in drawing the table up. (i) A single cell has its response field tuned (organised) by its own direct input, and indirectly (through a process of lateral or reciprocal inhibition) by the input to other cells whose preferred stimuli are similar to its own (cf Blakemore and Tobin, 1972; Carpenter and Blakemore, 1973). In other words, a stimulus is itself instrumental in determining the receptive field organization or response selectivity of neurones in visual cortex. (ii) Without the appropriate stimulation, a cell whose preferred stimulus ~~is~~ is a contour or edge, will respond to diffuse stimulation to an intermediate level. (iii) The amplitude of the evoked potential will reflect the level of activation (firing rate) of an aggregate of cells and/or the size of the population of cells so activated (cf Thompson and Bettinger, 1970; Thompson, Bettinger, Birch, Groves and Mayers (1969).

It can be seen that the critical cell in each case is Cell d. In the first condition it is envisaged to respond at an intermediate rate to the intermittent illumination of the left eye. The other cells that are capable of responding to information from this eye respond at the same rate. With the introduction of the horizontal grating to the right eye (Condition 2) Cell d has its receptive field finely tuned, with the effect that responding to changes in luminance is now precluded. Cells a-c behave as in Condition 1. The net result is a reduction in the amplitude of the evoked potential.

For Conditions 3 and 4 this same cell is again the critical one. In the former condition it is capable of responding to the changing luminance level of the left eye field, as in Condition 1, though not to the structural information therein, since this deviates substantially from its preferred stimulus. Cells a and c have their receptive fields tuned by the vertical grating and actively respond to the edges residing in the grating. In the fourth condition the situation changes.

As in the transition from Condition 1 to 2, Cell d becomes sharply tuned and incapable of responding to changes in luminance, with the result that a reduction in evoked potential amplitude again occurs. The dichoptic interaction observed in these studies need not, therefore, reflect the behaviour of a reversible inhibitory process of a kind that may underlie binocular rivalry. Rather, as Lehmann and Fender (1968) suggest, these effects may reflect an increase in the information loading of binocular elements by the structured field, which leaves less capacity for the contralateral light flashes.

That the behaviour of binocularly-driven cells is critical to the dichoptic interaction under consideration, is strongly supported by the results of a further experiment by Lehmann and Fender (1969). In a repeat of their previous experiment (cf Lehmann and Fender, 1967) a subject with a traumatic split of the chiasma was employed. This injury ensured that the primary visual cortex did not include units receiving binocular input. As would be predicted from the discussion relating to Fig 12, there was no evidence for any change in the amplitude of the evoked potential with the contralateral presentation of a structured target. Apart from assigning a critical role to binocularly-driven cells, this result eliminates an explanation of the dichoptic interaction in terms of general changes in retinal or cortical excitability.

One principle that emerges from these first studies is that presenting different images to the two eyes serves to prevent potentially binocularly-driven cells from responding simultaneously to the information originating in <u>both</u> eyes; whether this information relates to changes in luminance or to changes in structural content. Thus, referring to Fig 12 again, we see that Cell d is incapable of responding to the changing luminance in the left eye field because it is 'tuned' to respond very selectively by the preferred stimulus in the right field. It is incapable of responding to the structural information in the left field (Conditions 3 and 4) because this deviates from its preferred stimulus.

We may conclude, therefore, that the dichoptic interaction

demonstrated in these experiments need not necessarily reflect underlying suppressive influences in which the information from one eye is reversibly 'switched-off' or blocked, either by the contralateral input directly or by some feedback mechanism. To this extent, it may be assumed that the interaction observed in these experiments is not involved in binocular rivalry.

3.5.3 Experiments involving changes in luminance and the alternations in binocular rivalry

A number of experiments involving similar 'stepwise' changes in luminance have focused on detecting changes in the evoked response that may correlate with the perceptual alternations in binocular rivalry.

Balen (1964) presented different text to the two eyes, with a flicker superimposed on the right field. When subjects were asked to first read one and then the other sample of text, it was observed that the evoked cortical response to the flicker was of greatest amplitude when the subject was reading the intermittently illuminated text. However, although Van Balen states that his results were significant (it is not clear what, if any, statistical analysis was applied) the data illustrated in his Fig 2 (op cit, p 442) certainly do not show any of the clear differences that one would expect. Cobb et al (1967a) have since failed to replicate the study, finding that the amplitude of the evoked potential did not depend upon whether the 'reading eye' or the contralateral eye received the flicker stimulation. Cobb et al (1967a) presented a number of further experiments which all failed to demonstrate a change in the evoked potential during the suppression of a flickering field.

In the first of these the authors presented subjects with a vertically-oriented square wave grating to one eye, and a similar though horizontally-oriented grating to the other. Subjects observed the spontaneous rivalry between the two gratings and alternately closed two switches to indicate the currently-dominant field. In the binocular condition the flicker stimulation of the two eyes was temporally 180 deg out of phase, and Cobb et al reasoned that if the phenomenal suppression of one image is not accompanied by the loss of the corresponding evoked response the monocularly-derived responses should interact to cancel each other. Indeed, this was found to be the case, confirming that the currently-suppressed field contributed a fully-developed evoked cortical response to the EEG.

In their second experiment only one field was intermittently illuminated, and the intensity of the contralateral field was adjusted so that about equal periods of suppression of the two eyes were obtained. Cobb et al again failed to find a change in the evoked response to flicker that could be correlated with the individual phases of suppression of the intermittently-illuminated field.

Finally, in their third experiment Cobb et al had subjects reporting the rivalry alternations between two gratings that were both steadily illuminated. It was arranged that a single flash would be directed at one of the fields immediately after the subject had indicated that one or the other eye became dominant. Confirming the previous results, no consistent differences were observed in the evoked responses to the flash that could be related to the corresponding field's state of dominance.

All three experiments suggest, therefore, that the evoked response to luminate change is separable from perceptual experience: whilst the latter was found to be suppressed during rivalry, the former remained unaffected. This pattern of events contradicts the passive approach. However, in view of the results from a further study, this conclusion appears to be unjustified. Riggs and Whittle (1967) confirmed Cobb's findings in an experiment that in all essential details replicated his second experiment. Riggs and Whittle refer, however, to the disadvantage of using the stimuli they did, since "during the disappearance of the intermittently-illuminated field, considerable sensation of flicker remained". For these authors, therefore, the perceptual 'suppression' was clearly restricted to the structural content provided by the grating. In a personal communication to the writer, Cobb has reinforced these suspicions, stating that "...in our experiments the patterns showed rivalry while the flicker was perceived all the time" (underscoring mine). Thus, unless the potentials that were recorded can be related exclusively to the structural content provided by the grating, the experiments lose much of their significance. It is of no surprise to discover that an evoked potential can be recorded to changes in luminance that are

continually perceived. What is significent, however, is that these reports have consistently failed to demonstrate even a reduction in the amplitude of the evoked response to a suppressed field. To this extent the studies are valuable.

To summarize, the experiments reviewed in this section have failed to reveal a correlation between the presence/amplitude of the evoked potential and the phenomenal suppression of a flicker illuminated stimulus. Whilst the results have been consistent in this respect, doubt remains concerning the extent to which the perception of flicker per se was suppressed. The evidence does suggest that only the structural content of the intermittently-illuminated fields was phenomenally suppressed. In this case it is not surprising that an evoked potential to the flicker per se survived the suppression of a field. What is important, however, is that not even a reduction in the evoked potential was observed. Since there is evidence that with the flash illumination of a structured target, a pattern-evoked potential does contribute substantially to the EEG (MacKay and Jeffreys, 1973; Spehlmann, 1965; Regan, 1972; Rietveld et al, 1967; Jeffreys, 1968, 1969; Harter and White, 1968; John, Herrington and Sutton, 1967), it would seem that the evoked potential and a subject's perceptual experience can be dissociated. Whilst the perception of the grating itself was suppressed, that component of the evoked response which derives from the structural content was fully evident. In terms of the two approaches toward rivalry, these data therefore support the second, active approach, indicating that the processes responsible for dominance in rivalry lie more 'central' than the point at which the pattern-evoked cortical response is generated.

3.5.4 Experiments involving the presentation of structural information during binocular rivalry

In an attempt to record evoked potentials tp pattern, independently of luminance, a number of researchers have deviated from the traditional procedure of flash-illuminating a structured field. The first moves in this direction were made by Riggs et al (1964 ; Johnson et al 1966) who recorded the ERG to the movement of a pattern of alternating bars that differed solely in terms of intensity or colour. By means of an oscillating mirror, these patterns were made to move to and fro through one bar width, so that with each movement the patterns reversed. Gross et al (1967) used a similar stimulus in an investigation of the suppression of the evoked response during voluntary eye movements. In their study the subject viewed a pattern of equal light and dark stripes for which could be abruptly substituted a similar pattern that was spatially out of phase.

Riggs and Whittle (1967) presented a diagonally-oriented square wave grating to a subject's left eye, and a similar though vertically-oriented grating to his right eye. Each field subtended 10 deg and contained 8 black and 8 white stripes. The vertical grating was made to reverse at a rate of 25/sec and subjects reported which field was currently dominant during the rivalry. Whilst the phenomenal suppression of the reversing pattern was complete in this instance, there were no changes in the evoked potential with which it could be correlated.

Cobb et al (1967b) undertook a similar experiment. Again, subjects were presented with gratings that were differently oriented for the two eyes, and again one of these was made to reverse (rate = 6/sec). Whilst reporting a change in the evoked potential that was correlated with the reversing field's suppressed phases, it was the case that a potential could clearly be distinguished in the EEG.

Consistent with these data are two studies which, though bearing on the problem of the physiological processes underlying rivalry,

have not previously been related to the phenomenon.

In the first study, Campbell and Maffei (1970) presented circular fields, subtending 2 deg visual angle, to the two eyes. The two fields contained differently-oriented square wave gratings - vertical and horizontal. They employed a continuous alternation in the pattern (ie pattern reversal) at a frequency of 8c/sec. The fields were made to alternate simultaneously and <u>in</u> phase.

The authors were interested in determining whether the evoked potential would provide evidence for the existence of channels that were selectively sensitive to orientation. They reasoned that if such channels exist, then the responses to two quite differently oriented stimuli should not interact; each should be capable of developing fully without interference from the information in the other channel. They predicted, therefore, that when presenting a subject simultaneously with differently-oriented gratings, the evoked potential would reflect their independence by showing a summation of the 'two' evoked potentials. In order to provide this evidence for summation, they focused on the function that relates stimulus contrast to the amplitude of the evoked potential - a function that is described by a straight line. They predicted, therefore, that should there be separate channels, the evoked potential should display a summation of the response which, in turn, would be reflected in a function, relating contrast with amplitude, having a regression coefficient (slope) twice as large as that obtained under conditions of monocular stimulation, obtained with just the single orientation. They obtained this result and concluded that the activity in two <u>separate</u> (independent) orientation channels had summed.

Whilst it must be remembered that Campbell and Maffei do not report whether the subject experienced perceptual suppression of part or the whole of one field, one must assume from Riggs and Whittle (1967) and Cobb et al (1967a, b) that this was a likely outcome.

It may be noted in addition, that their result is entirely consistent with the scheme illustrated in Fig 12. As was argued above,

presenting disparate structural information to the two eyes serves to segregate the 'binocularly'-driven cells into left and right eye responsive.

In the second study Ciganek (1973) also failed to report upon subjects' perceptual experience when presenting different structural information to the two eyes. When patterns, whose elements were small enough to ensure that no component of the evoked potential was attributable to changes in luminance, were tachistoscopically-presented, he found that the evoked potential resulting from the dichoptic presentation of dissimilar stimuli reflected the 'addition' or summation of the component responses; the responses deriving from each of the monocular inputs. The patterns employed would not be expected to fuse and so, again, we have evidence for the independence of the two monocular channels under conditions of dichoptic presentation.

3.5.5 Negative Evidence

The studies reviewed in the last two sections have been consistent in demonstrating the existence of a pattern-evoked potential to a stimulus that is perceptually suppressed in binocular rivalry. There are two further studies, however, that have provided rather different results.

In a study involving reversing gratings, Cobb et al (1967b) employed a condition of simultaneous, out-of-phase stimulation of the two eyes. They observed that the temporarily suppressed field did not contribute an evoked potential to the EEG; that is, the response to the reversal of the currently-dominant field was not influenced by the contralateral field. And, though they did not use stimuli that alternated in dominance (rather one field suppressed the other continuously) van der Tweel et al (1970) provided data that are consistent with these results. They found that a reversing chess-board pattern of low contrast that was viewed by one eye, was suppressed by a static chessboard pattern of identical square size and high contrast that was viewed by the other eye. Making the static field smaller in overall size than the reversing one, van der Tweel et al rather cleverly showed that the amplitude and distribution of the evoked potential, obtained when a region of the reversing field was suppressed, were the same as those obtained when an idential region was physically cut off. The amplitude and distribution of the evoked potential reflected the perceptual suppression in this study.

3.5.6 Conclusion

With respect to the two alternative approaches toward rivalry outlined earlier, the studies that have been reviewed, with two exceptions, favour the second of these since it does not preclude the continued cortical analysis of currently (phenomenally) suppressed information. Since a number of studies assign a major discriminatory role to visual cortex, it may be concluded that the weight of evidence points to the continued discrimination of currently-suppressed material.

3.6 EXPERIMENT 4 THE SELECTIVE EFFECTS OF RIVALRY SUPPRESSION ON THE CORTICAL EVOKED POTENTIAL

There are a number of possible explanations for the discrepant findings of the last two studies. Consideration of the most likely serves to suggest a more useful manner in which the evoked cortical potential may be employed in an investigation of binocular rivalry.

Firstly, it is not essential to assume that regular changes in a stimulus are signalled by neural activity that is time-locked to them. Fukada et al (1966) have recorded activity from the optic nerve of cat, which, although correlating with the presence of flicker, was not time-locked to the stimulus. This may be understandable when one considers that, at least for stimulus repetition rates exceeding 5-7 Hz, the subjective impression of flicker grows vague and, in general, seems lower than that of the physical stimulus. For these reasons it may be unreasonable to always anticipate a correlation between perception and phase locked evoked potentials.

Secondly, by employing steady-state rather than transient potentials, and by omitting to vary stimulus frequency systematically, these two studies may simply be reflecting the selective nature of changes in cortical activity. There is evidence to indicate that the steady-state evoked potentials obtained at different stimulus frequencies are to some extent independent. Thus, evoked potential components in the ranges 45-60, 12-25 and 10 Hz have different latencies, topographical distribution, and relationship with stimulus colour (Regan, 1972). Selective changes in the evoked potential would be understandable if it were to be assumed, in line with the active approach to perception, that the process that is the basis of perception contributes to the potential: "....the evoked potential components which (in MacKay's view) reflect matching activity might be expected to correlate closely with the subject's perception of the stimulus. On the other hand, evoked potentials which reflect the form of peripheral neural signals might be expected to correlate poorly with perception" (Regan, 1972, p 34).

Since there have been a number of successful attempts to divide the transient evoked potential waveform into components of different latencies, and to relate these to different functions of the central nervous system and to different brain structures, the transient potential recommends itself as the more appropriate tool for investigating the changes that may accompany the suppression in rivalry.

That changes in evoked cortical activity accompanying visual suppression might indeed be restricted to certain components of the evoked potential is suggested by a number of studies that have employed transient rather than steady-state potentials. Perry, Childers and Dawson (1969) presented, tachistoscopically (10 msec exposure), differently-coloured stimuli under monocular, dioptic and dichoptic viewing conditions. The colours employed were red, green and yellow. In the dichoptic condition (ie with a different colour presented to each eye) Perry et al observed that it was only the later components of the transient evoked potential (latency 215+ msec) that reflected the integration or fusion of the red and green fields to yield 'cortical yellow'. Moreover, they found that colour coding per se occurred with respect only to the later components, indicating that if any aspect of the evoked potential is to be correlated with a subject's perceptual (phenomenal) experience, it must be these components.

Hartley (1968) presented a blank flash to one eye during the continuous presentation of a subliminal stimulus to the other eye; a stimulus that was either a neutral or unpleasant word. He found that the unpleasantness of this latter stimulus caused a reduction in the evoked potential to the flash, and that this reduction was restricted to the later components (approx 280 msec latency).

Finally, Lawwill and Biersdorf (1968) employed a slow rate of flicker illumination of rivalling gratings that effectively gave rise to a transient response. The frequency of illumination was different for the two eyes, permitting the simultaneous recording of information from each eye. These authors observed that it was a reduction in the amplitude of a longer latency (280+ msec) component that accompanied suppression.

There seems, therefore, to be some justification for thinking that the evoked potential changes that may accompany the suppression in rivalry will be selective and, more specifically, be restricted to the later components. The possible involvement of the later components in rivalry suppression makes particularly good sense in terms of the active approach toward rivalry. Thus, whilst the earlier components of the potential have been linked with the cortical discrimination or analysis of a stimulus (Jeffreys, 1968; 1969), these later components have been associated with more active or endogenous processes and with perceptual experience.

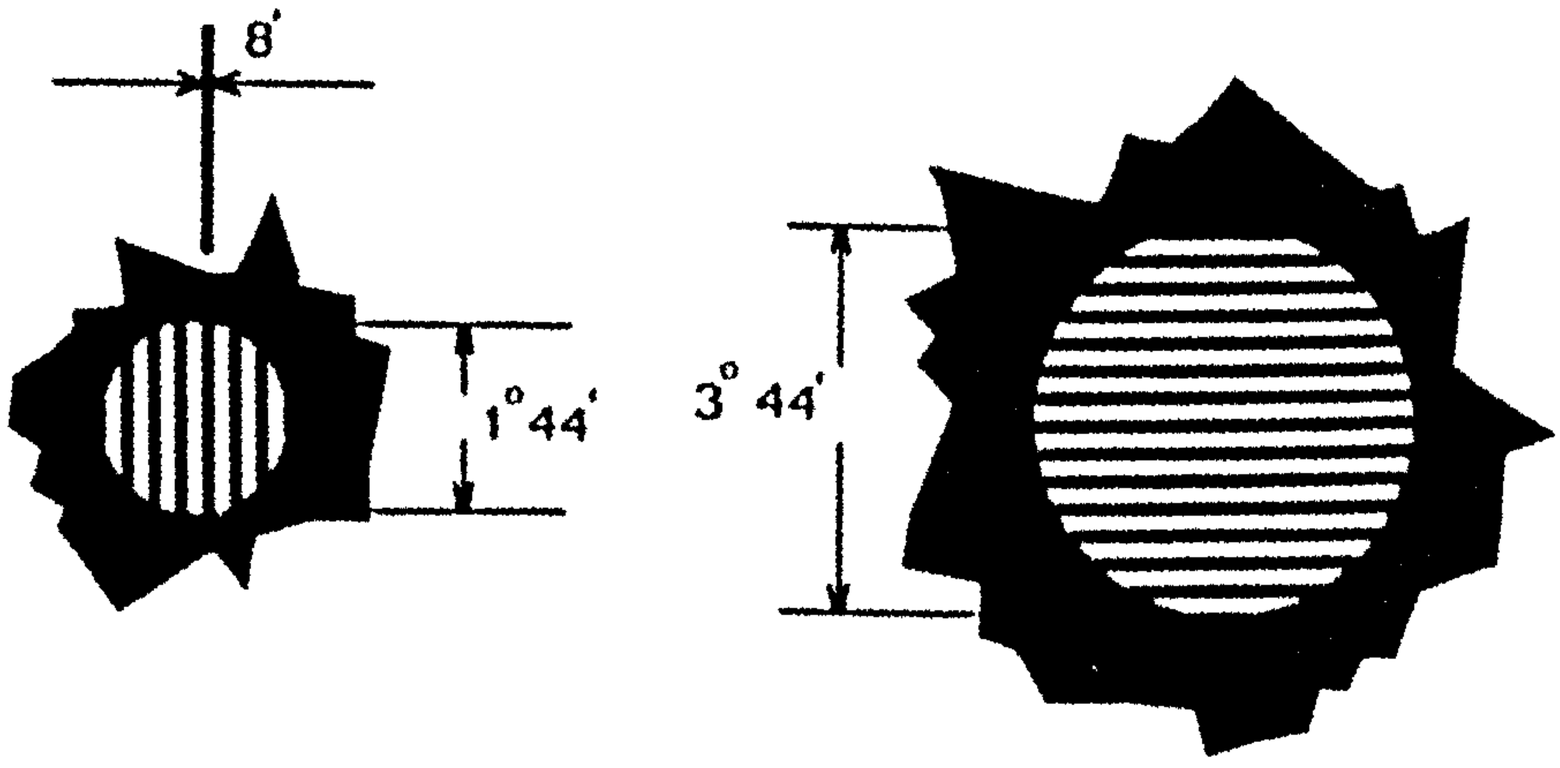
With these points in mind an experiment was designed that involved pattern-specific information, and transient rather than steady-state evoked potentials. In line with the active approach toward rivalry it was predicted that the (early) components of the evoked potential, that appear to reflect the cortical discrimination of a stimulus, would be unaffected by the temporary state of suppression of a rivalling field. Whilst, in contrast, it was predicted that the later components, that are believed to correlate more directly with perceptual experience, would differentiate the suppressed and dominant status of a stimulus by being absent, markedly reduced and/or delayed in the former case.

METHOD

Subjects observed the rivalry alternations between two continuously illuminated square wave gratings that were differently oriented for the two eyes - vertically and horizontally for the left and right eye respectively (cf Fig 13). Evoked responses to the pattern reversal of the vertical grating were recorded under three different conditions: (i) whilst there was no competing stimulus presented to the right eye (monocular condition); (ii) whilst, when both gratings were illuminated and appearing to rival, the vertical grating itself was reported by the subject to be dominant (dominant condition), and (iii) whilst the vertical grating was reported to be temporarily suppressed (suppressed condition). Each subject served as his own control, contributing an averaged evoked potential under each of the three conditions. An equal number of subjects undertook the trials in each of the two orders that were employed, viz. monocular-dominant-suppressed, and suppressed-dominant-monocular.

Figure 13

The vertical and horizontal square wave gratings that were presented to subjects' left and right eyes respectively.


8'
1°44'
3° 44'

The moment at which the grating was reversed was, within certain limits, randomly determined on each occasion. More specifically, the grating was reversed after a quasi-random time interval (lying between 0.9 and 0.15 sec) from the subjects reporting that the vertical grating had returned to a dominant or suppressed status (depending upon the condition). If within this time interval the vertical grating changed status yet again, its reversal was cancelled.

The randomness of the time interval served to preclude contamination of the evoked potential by non-visual factors (cf Vaughan, 1969a); factors likely to accompany the binocular rivalry alternations themselves, or the subjects reporting of these. Such factors may include the motor potentials associated with the subjects' manual response to the change in dominance, the long latency responses associated with the decision processes accompanying the manual reports, and any extra-cranial responses such as the electroretinogram and electro-oculogram that accompany the alternations in rivalry.

SUBJECTS

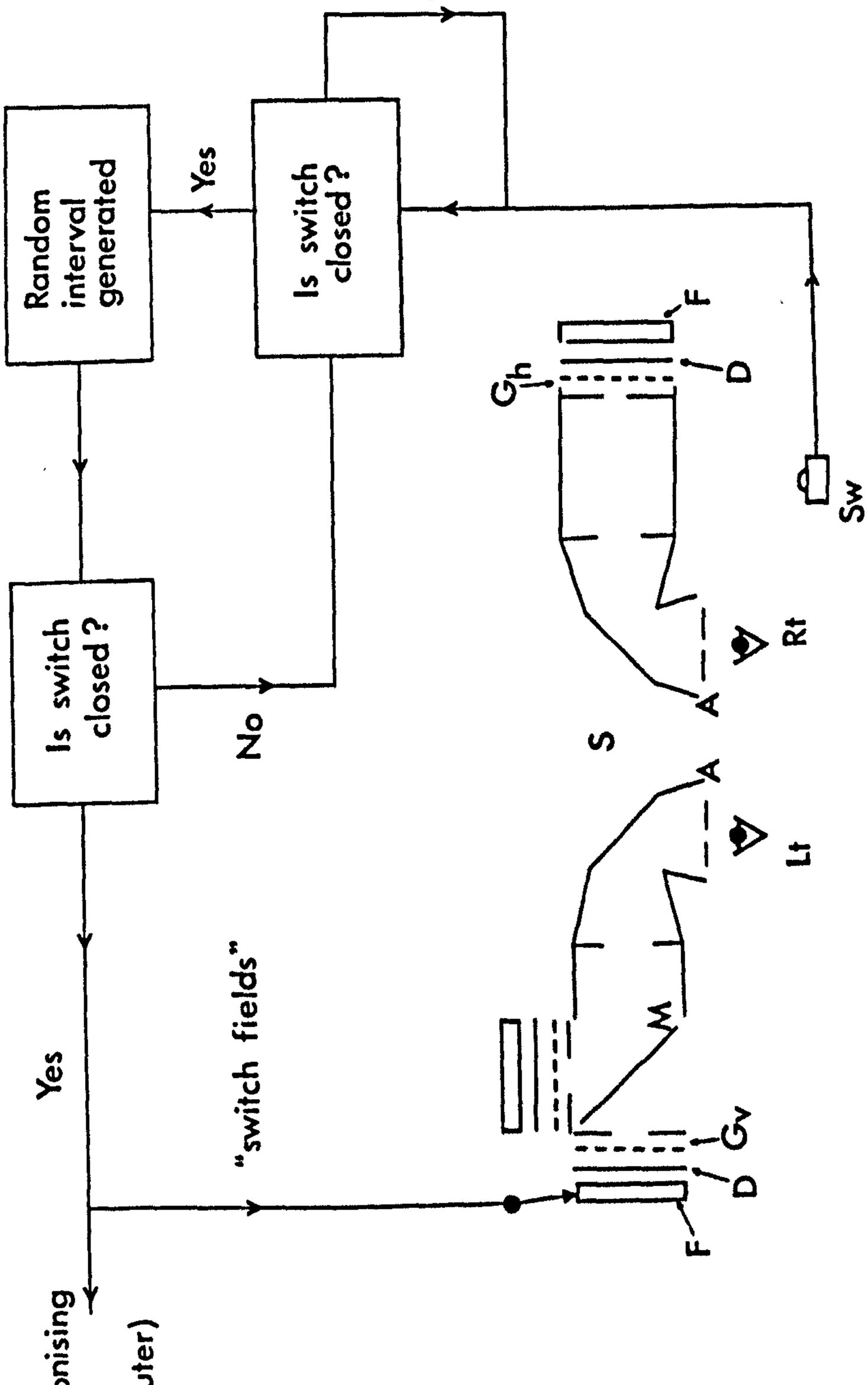
Fourteen subjects, varying between 21 and 27 years, participated in the experiment. All had visual acuities equal to or better than 20/20 and were capable of displaying a readily detectable alpha component in their EEG.

APPARATUS AND VISUAL STIMULI

The square wave gratings were produced from commercial Letraset applied to standard white paper, and consisted of black and white 'stripes' of equal width. The density of contour in the two gratings, as measured by the angle subtended by the individual 'bars', was 12 min. The angles subtended by the circular fields within which the gratings appeared were 2 deg 36 min and 5 deg 36 min for the left and right eye-fields respectively. The difference in overall size of the two fields served to discourage the appearance of a piecemeal form of rivalry, in which different localized parts of the stimuli appear to behave independently.

Figure 14

Schematic representation of the apparatus and functioning of logic equipment. A, artificial pupils; S, synoptophore; Sw, switch (push-button); Gv, Gh, vertical and horizontal gratings; D, diffusing screen; F, flourescent discharge lamps; M, half-silvered mirror; Lt and Rt, subject's left and right eyes.


Random interval generated
Yes
Is switch closed?
Is switch closed?
No
Yes
"switch fields"
synchronising signal (computer
F
Gh
D
Sw
A
S
Rt
A
Lt
M
Gv
D
F

Visual stimulation was controlled by a synoptophore that was specially adapted for the experiment. The original light sources were removed from the instrument and the arms extended to give an effective viewing distance of 30 cm. As substitutes for the original light sources, Philips TL 6W/33(cold) lamps were positioned so as to back-illuminate the gratings. Placed between each light and its grating was an opal perspex diffusing screen (3 mm in thickness). Artificial pupils (2 mm diameter) were added to the synoptophore and head movements were minimized with chin and forehead rests. The lighter parts of the gratings had a luminance of 1.5 log ft lamberts.

The reversal of the vertical grating was effected by having two identical gratings presented to the subject's left eye, one of these via a half-silvered mirror. Whilst only one of these could be illuminated at any time, a switch could be quickly made from one to the other. Though identical, the two gratings were placed within their apertures so as to be spatially 180 deg out of phase. In this way, transferring from one to the other provided the pattern reversal to which a visual evoked potential was to be recorded. With very fast rise times for the lamps ($3 \pm .2$ msec) structural information was provided in the absence of any change in overall luminance.

A single push button was provided for each subject for use with his right hand. Depression or release of this button (depending upon the condition) indicated whether the current state of the rivalry was appropriate for a pattern reversal to be initiated. "Devices" logic equipment then defined the time interval between button depression and pattern reversal, with the condition that a reversal would not occur if a rivalry alternation occurred during this interval. In addition to initiating the reversal, the logic equipment delivered a synchronizing signal to the computer to define the start of the 1,500 msec sampling-and-averaging period.

Attempts were made to eliminate possible contaminating stimuli. Thus, the logic equipment (cf Fig 14) that triggered and controlled the pattern shift, was housed in an adjacent room and within a small, tight-fitting sound-proof cabinet. Any auditory cues accompanying the

sequencing were thus eliminated. The additional precaution was taken of removing the Dynagraph pen, that signalled the occurrence of a reversal, from its harness. This eliminated any sound of pen-movement on the paper chart of the Dynagraph (the subject was positioned a matter of only 1.5 metres from this piece of equipment). Proper grounding of the equipment, in addition to the use of screened mains leads, helped eliminate electrical interference.

A pair of scalp electrodes (silver/silver chloride cup electrodes) were arranged for bi-polar recording over the occiput, 2 cm to the right of the midline. One electrode was placed level with the inion and one was placed 4.5 cm above this. A wrist contact (attached to the subject's left wrist) served as the ground electrode.

Cortical activity was amplified by an Offner Dynagraph (type RC). A PDP-12 laboratory computer averaged the cortical activity for 1,500 msec following stimulation, with 90 samples (sweeps) contributing to each average. A number of optional subroutines provided facilities in addition to the averaging function. These included: (i) a display on the CRT of a sample-by-sample average, permitting an informal visual assessment of the variability associated with the final average; (ii) a display of the most recent sample of EEG, which permitted the contribution of movement and other artifacts to the EEG to be assessed. The final average evoked potential was transferred for permanent storage to magnetic tape, and for immediate analysis to a paper chart, via a George Washington 400 MD2 two-channel direct oscillograph.

PROCEDURE

The subject was first reassured as to the safety of the procedures associated with recording evoked potentials.

The areas of the scalp to which the electrodes were to be attached were cleaned with ether. The cup electrodes were fixed in position by means of Collodion glue and an S L E air gun speeded its drying. To reduce contact resistance a quantity of electrode jelly was inserted beneath the electrode 'cup'. The blunted needle of the syringe that

was used to apply the jelly was first used to abrade the skin in order to further reduce the inter-electrode resistance.

After placement of the electrodes, the subject was introduced to the apparatus. With both fields illuminated the subject adjusted the synoptophore until they appeared superimposed (concentric). The subject was next asked to relax and steadily fixate the centre of the patterns, and to describe what he saw. He was allowed to discover for Himself the rivalry between the two fields. The experimenter did not attempt to explain the illusory nature of the phenomenon but rather simply referred to the 'disappearance' and 're-appearance' of the vertical grating.

It was next checked that the placement and contact of the electrodes were satisfactory, and that the subject was comfortably positioned when viewing the rivalling fields. Thus, with the subject positioned to view the two fields of the synoptophore, but with his eyes closed, the EEG trace was inspected for the presence of muscle spindles and alpha waves. Whilst the former were eliminated as far as was possible (the position of the chin and forehead rests could be altered, and the height of the table upon which the synoptophore rested was adjustable), the presence of the latter helped confirm that the electrodes were making good contact with the scalp and that the subject could relax.

The subject was next given a practice trial, lasting 3 minutes, that was preceded by the instruction "Look into the apparatus, all the time fixating on the centre of the stimulus and maintaining a relaxed state. As you have already observed, the vertical grating (ie the circle of vertical lines) may disappear and reappear. All that I want you to do is press this button, with your right index finger, whenever and for as long as the grating is there. Whilst it is not there do not press the button at all. Do you understand what you are to do?"

During this practice trial the subject's responses on the push-button had no effect on the vertical grating, ie there were no reversals of the grating.

For both the dominant and suppressed conditions the instructions given the subject were essentially as for the practice trial. Again the subject pressed the key to indicate the dominance of the vertical grating. The difference between the two trials lay in the internal configuration of the logic equipment. Depending upon the experimenter's positioning of a simple switch, the sequence of events leading to a pattern reversal was initiated either by a key press (dominant condition) or by a key release (suppressed condition).

For the monocular condition the subject was asked to approximately reproduce his responses on the practice trial; that is, to imagine that the horizontal grating was present and that the vertical grating was disappearing and reappearing, and to press the button accordingly. During this trial the horizontal grating was not illuminated.

Between each trial the subject was allowed a five-minute rest period, during which he was asked to describe the behaviour of the gratings on the previous trial. No feedback as to the appropriateness of this behaviour was given. After all trials had been completed the purpose of the experiment was explained to the subject.

		Component			
		1	2	3	4
Source	D.F.	S.S.	S.S.	S.S.	S.S.
Between subjects	13	9.93	20.98	35.67	10.76
Within subjects	28	5.68	10.98	17.21	32.14
C	2	0.05	0.94	3.05	8.13
C x subjects	26	5.63	10.04	14.16	24.01
Total	41	15.61	31.97	52.88	42.90

Multiple comparison tests (df=1,26):

Component 3 C_1 vs. C_2 - F=1.536, n.s.

(C_1+C_2) vs. C_3 - F=4.106, P 0.05

Component 4 C_1 vs. C_2 - F=0.292, n.s.

(C_1+C_2) vs. C_3 - F=8.564, P 0.01

Results of analyses of variance on the amplitude of the four components of the evoked potential to the complete reversal of the vertical grating, and the results of the multiple comparison tests involving the components yielding significant results.

The C factor refers to the different conditions under which the potentials were obtained. C_1, C_2 and C_3 referring to the monocular, dominant and suppressed conditions respectively.

Table 15

		Component			
		1	2	3	4
SOURCE	D.F.	S.S.	S.S.	S.S.	S.S.
Between subjects	13	33.92	45.05	38.38	46.35
Within subjects	28	11.16	14.42	19.61	24.66
C	2	1.13	0.03	6.54	8.62
C x subjects	26	10.03	14.39	13.07	16.04
Total	41	45.08	59.47	57.99	71.01

Multiple comparison tests ($df = 1,26$):

Component 3 C_1 vs. C_2 - $F=0.62$, n.s.

(C_1+C_2) vs. C_3 - $F=12.42$, $P < 0.01$

Component 4 C_1 vs. C_2 - $F=0.00$ n.s.

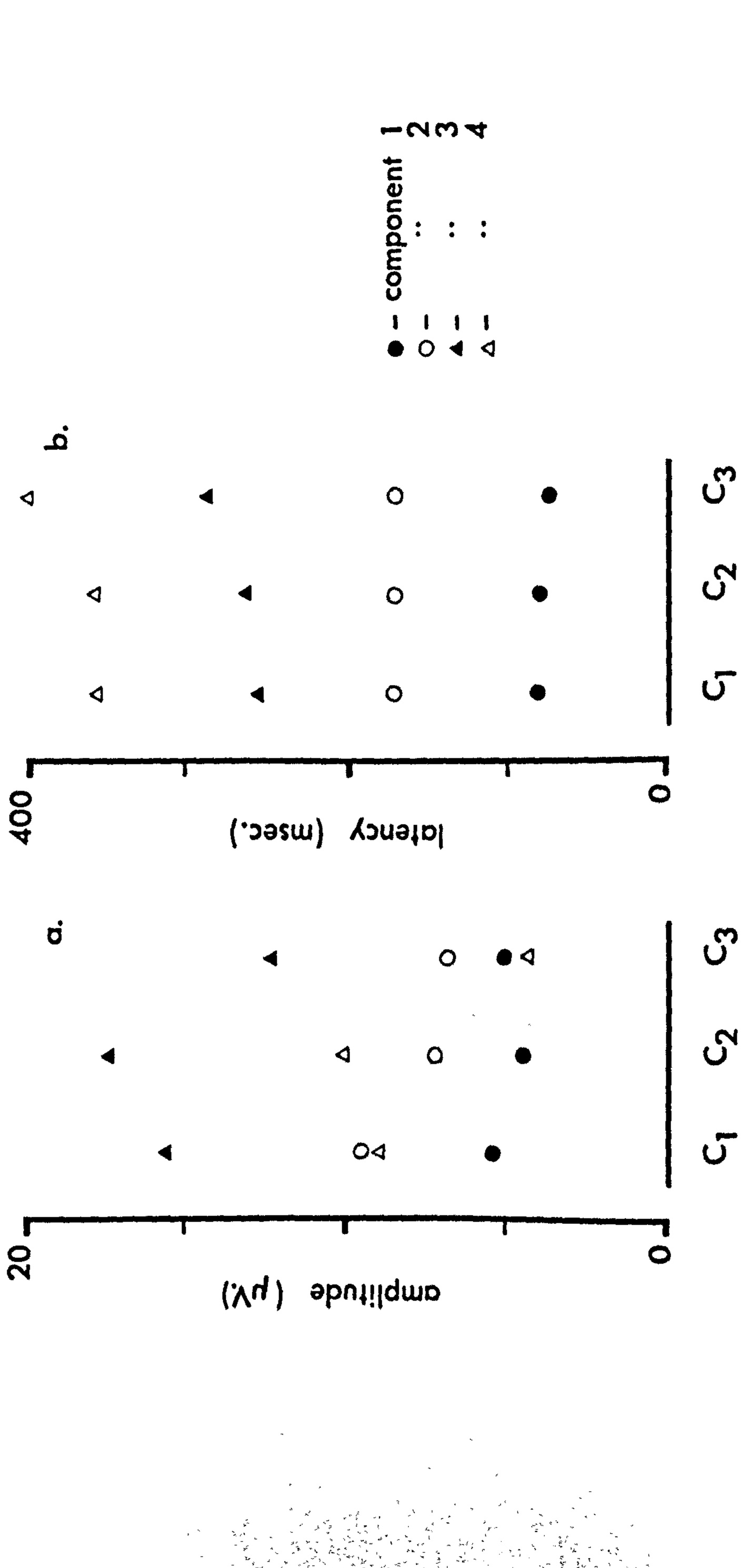
(C_1+C_2) vs. C_3 - $F=18.52$, $P < 0.01$

Results of analyses of variance on the latency of the four components of the evoked potential to the complete reversal of the vertical grating, and the results of the multiple comparison tests involving the components yielding significant results. cf. Table 15 for code.

Table 16

Figure 15

Mean values, averaged over subjects, for the amplitude (a) and the latency (b) of the four components of the visual evoked potential, in the three conditions of experiment 4.
C1, C2 and C3, the normal, dominant and suppressed conditions respectively.


component 1
2
3
4
b.
latency (msec.)
400
0
C_1 C_2 C_3
a.
amplitude (μV)
20
0
C_1 C_2 C_3

RESULTS AND ANALYSIS

All fourteen subjects reported that they experienced binocular rivalry and that the task of reporting the alternations was not too difficult. All subjects were confident that their manual reports were reliable. Furthermore, the shifts in dominance were sufficiently abrupt as to not cause any ambiguities. Rather unexpectedly, subjects invariably reported that, in the suppressed condition, the vertical grating quickly reappeared, albeit relatively slowly at the beginning of the trial, only then to speed up. Although returning quickly, no subject reported seeing the reversal of the vertical grating.

Data from four previous reports (Harter, Seiple and Salmon, 1972; Beck, Dustman and Sakai, 1969; Vaughan, 1969a; Jeffreys, 1969) provided a basis for expectations as to the morphology of the transient evoked potential to the pattern reversal. Whilst all four studies give evidence of substantial variation between subjects, all concur in revealing four major components to the visual evoked potential. The first two early components are negative and have latencies in the ranges 80-110 msec and 120-200 msec. The later two components are positive and have latencies in the range 200-400 msec. The first three of these components were objectively defined and validated by a method of variance analysis (Harter et al, 1972). Harter et al found that these first three components (i) reflected the changes in evoked potential waveform that occurred as a function of their experimental conditions, (ii) were appropriate for the majority of subjects, and (iii) were to be clearly distinguished in previous investigations of pattern evoked potentials (Spehlmann, 1965; Rietveld et al, 1967; Harter and White, 1968; 1970; White, 1969; Lundlam and Meyers, 1972). Importantly, the identification of these principal components implies that baseline-peak measures of amplitude are more appropriate than peak-peak measures, since separate neural processes appear to underlie positive and negative components. The problems associated that this measure must be borne in mind, however, viz. (i) defining the baseline, (ii) allowing for the fact that, for example, a negative-positive going peak may be displaced bodily into the positive region by a simultaneously-occurring positivity, and (iii) an apparently single peak may be composed of two separate components (Regan, 1972, p 229).

Upon inspection of the obtained evoked potentials it was clear that there were large individual differences in morphology. Nevertheless, in most cases components could be discerned at approximately the above latency ranges. In an attempt to provide objective measurement of the potentials, an independent judge was given the chart record copies in a random and 'blind' manner, in addition to the following instructions: "Inspect each record of an evoked potential. First fit a baseline through the beginning half-second of each trace. Isolate the most negative point of the EEG trace within the latency range 60-110 msec and the most negative point in the range 110-200 msec. Isolate the two most positive points in the potential with the range 200-500 msec. When these have been isolated, measure their peak-baseline amplitude (the judge was provided with a 10 mV calibrating record) and latency".

Analyses of variance appropriate for repeated measures designs were undertaken on the values provided by the judge. After the square-root transformation of these values a separate analysis was applied to the data for each component. Supplementing the main analysis, multiple comparisons were undertaken in order to detect significant differences between the means from the different conditions.

For the amplitude data, Table 15 shows each summary analysis of variance and the results of the multiple comparisons where these proved significant. Fig 15a illustrates the mean amplitude values in microvolts. Table 16 and Fig 15b indicate the same for the latency data.

The analysis indicated that there were no significant differences between the monocular and dominant conditions for any of the components. Furthermore, there were no changes in the earlier negative components that could be associated with the suppression of the vertical grating. Changes were observed, however, in the later components. These changes involved (i) a reduction in the amplitudes of the two later positive components, from 10.21 and 17.36 μV to 4.28 and 12.29 μV respectively (yielding corresponding F values df = 1,26, of 4.106, which just fails significance at 5% level, and 8.564, $P < 0.01$ respectively), and (ii)

an increase in the latency of these components, from 263.4 and 357 msec to 287.3 and 399 msec respectively (yielding corresponding F values, with df = 1,26, of 12.42, $P < 0.005$, and 18.52, $P < 0.005$ respectively).

Before discussing the results, two further experiments will be reported whose purpose was to provide additional controls.

3.7 EXPERIMENT 5 DETECTING STIMULUS-LOCKED ARTIFACTS

When recording evoked potentials it is necessary to control for stimulus-locked artifacts by recording averages under 'stimulus-off' conditions. Although every precaution had been taken to eliminate such artifacts, evoked potentials were recorded from a number of additional subjects under control conditions.

Only two trials were involved. In all essential details the conditions were as for the dominant condition of the preceding experiment. However, for the control condition the two vertical gratings were re-positioned within their fields so as to be phenomenally superimposed, thus ensuring that the transfer of illumination from one to the other did not involve a reversal in contrast or, indeed, any other change.

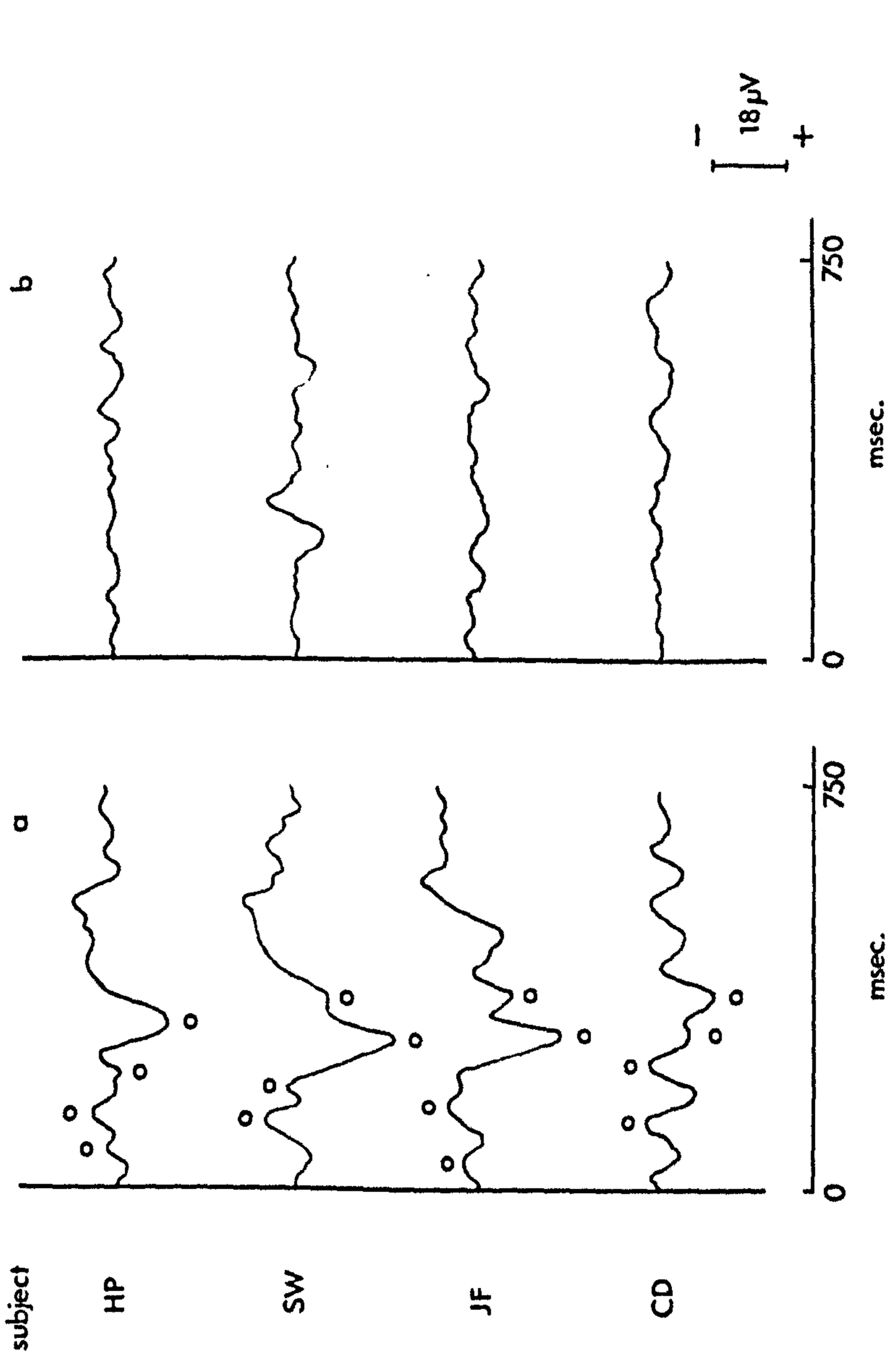
There were four subjects in all, varying in age between 22-24 years. All had visual ~~activities~~ acuities equal to or better than 20/20 and were capable of displaying a readily-detectable alpha component in their EEG. Two subjects completed the two trials in each possible trial order.

RESULTS

Each of the subject by condition average evoked potentials are illustrated in Fig 16. Shown in this figure, and indicated by the symbol 'o', are the components of the evoked potentials as identified by the instructions that were given to the judge in the previous experiment. The average latencies of these components were 95 msec (N1), 178 msec (N2), 265 msec (P3) and 346 msec (P4). Unfortunately, statistical tests for the presence of an evoked potential in the EEG have proved elusive (cf Regan, 1972). The most promising technique, recently described by Wienberg et al (1970) requires rather powerful computing facilities. Fortunately, visual inspection of the results indicates that only for the dominant condition were evoked potentials obtained. It may be concluded, therefore, that no significant stimulus-locked artifacts contributed to the results of the first experiment.

Figure 16

The evoked potentials obtained from the dominant (a) and control (b) conditions of experiment 5, from each of the four subjects.
"o" indicates the four components of the evoked potentials.


b
a
18μV
750
0
msec.
subject
HP
SW
JF
CD

3.8 EXPERIMENT 6 ELIMINATING AREAL CHANGES IN LUMINANCE AS A FACTOR CONTRIBUTING TO THE EVOKED POTENTIAL

When employing similar pattern reversal, Cobb et al (1967b) checked that the evoked potentials were 'contrast specific' by demonstrating (i) their sensitivity to visual accommodation, and (ii) that the shape of their amplitude vs frequency curve was characteristic of such potentials (cf Regan, 1972). In the way of providing a similar check, viz. that the evoked response did not reflect localized changes in luminance (changes in luminance level in an area contained within one 'bar' of the pattern), a further study was undertaken that in all essential details, except one, replicated the first experiment.

For this study the relative position of the two vertical gratings that were presented to the left eye was changed yet again. The gratings were positioned so that upon transferring illumination from one to the other, there was a lateral displacement of the grating (amounting to 3' visual angle) rather than a complete reversal in contrast.

There were six subjects, varying between 22-29 years. All had visual acuities of better than or equal to 20/20 and were capable of displaying a readily noticeable alpha component in their EEG. Three subjects undertook the experiment in each of the two trial-orders that were employed. The same colleague served as the judge in measuring the latencies and amplitudes of the components of the evoked potentials.

		Component			
		1	2	3	4
SOURCE	D.F.	S.S.	S.S.	S.S.	S.S.
Between subjects	5	3.57	11.80	7.88	3.92
Within subjects	12	4.11	7.24	8.57	16.18
C	2	0.02	1.59	2.25	9.58
C x subjects	10	4.11	5.65	6.32	6.60
Total	17	7.68	19.21	16.45	20.10

Multiple comparison tests (df=1,10):

Component 4 C_1 vs. C_2 - F=0.018, n.s.

(C_1+C_2) vs. C_3 - F=14.505, $P < 0.01$

Results of analyses of variance on the amplitude of the four components of the evoked potential to the incomplete reversal of the vertical grating, and the multiple comparison tests involving the component that yielded significant results. cf. Table 15 for code.

Table 17

		Component			
		1	2	3	4
SOURCE	D.F.	S.S.	S.S.	S.S.	S.S.
Between subjects	5	15.01	15.56	17.39	22.02
Within subjects	12	2.78	9.05	7.85	12.69
C	2	0.32	0.91	3.60	7.32
C x subjects	10	2.45	8.15	4.25	5.37
Total	17	17.79	24.61	25.23	34.71

Multiple comparison tests (df=1,10):

Component 3 C_1 vs. C_2 - F=0.146, n.s.

(C_1+C_2) vs. C_3 - F=8.29, $P < 0.05$

Component 4 C_1 vs. C_2 - F=0.089, n.s.

(C_1+C_2) vs. C_3 - F=13.549, $P < 0.01$

Results of analyses of variance on the latency of the four components of the evoked potential to the incomplete reversal of the vertical grating, and the results of the multiple comparisons involving the components that yielded significant results, cf. Table 15 for code.

Table 18

		Monocular	Dominant	Suppressed	
Component	1	6.58	6.9	7.8	
	2	10.15	7.3	7.05	
	3	13.50	15.8	9.9	a.
	4	8.65	9.53	1.18	
	1	74.3	75.8	71.3	
	2	169.0	180.7	169.8	
	3	260.5	256.0	290.0	
	4	356.0	360.3	410.3	b.

Values for (a) the amplitude (mVolts) and (b) the latency (msec.) of each of the four components of the evoked potential to the incomplete reversal of the vertical grating in the monocular, dominant and suppressed conditions.

Table 19

RESULTS AND ANALYSIS

Tables 17 and 18 show the summary analysis of variance tables and the results of the multiple comparisons (where these are significant) for the amplitude and latency data respectively. Table 19 gives the mean component by condition values.

The results of the analysis were essentially as for the first experiment. There were no changes in the two early components across any of the conditions, in terms of either latency or amplitude. A comparison of the dominant and monocular conditions similarly revealed no differences in the later components. As in the first experiment, the only changes in evoked potential were associated with the suppressed condition and with the later components. There was an increase in the latency of the third and fourth components ($F = 8.29$; $df = 1,10$; $P < 0.05$ and $F = 13.55$; $P < 0.01$ respectively) and a reduction in their amplitude, though only in the latter case did this attain significance ($F = 14.5$; $df = 1,10$; $P < 0.01$).

The results indicate, therefore, that areal changes in luminance were not important in the first experiment.

3.9 DISCUSSION OF EXPERIMENTS 4, 5 & 6

Consistent with the interpretation of previous evoked potential studies, there were no changes in the early components of the evoked potential that could be correlated with either the presence of a structured field to the contralateral eye (the monocular vs dominant comparison) or with the suppressed status of the vertical grating (suppressed vs dominance+monocular comparison). As far as the early components indicate, therefore, there is no interference between the two monocular systems in binocular rivalry. Since there is evidence to indicate that the early components reflect activity in striate cortex, and the discrimination of the physical properties of the stimulus (cf Regan, 1972; MacKay & Jeffreys, 1973), it may be concluded that the (cortical) discrimination of a stimulus continues despite its phenomenal suppression. To this extent the results are consistent with the active approach to binocular rivalry and perception in general.

If perceptual experience is to be correlated with the appearance of the later components (cf below) the fact that there were any components in the range 200-400 msec in the suppressed condition is perhaps surprising. Subjects in this condition confidently reported that they did not see the reversal of the grating. However, the subjects did report that in this condition the vertical grating, on disappearing, quickly reappeared, albeit relatively slowly at the beginning of the trial. Thus, there was a perceptual event with which the later components could be associated. Moreover, this association could possibly explain the reduction in amplitude since variability in the latency of individual components would cause a corresponding reduction in amplitude of the average. As has been mentioned, the reappearance of the vertical grating, though quick, did not seem to be rigidly synchronized with its actual reversal.

Although these rather immediate perceptual consequences of the pattern reversal make for some difficulties in interpreting the changes in the evoked potential, they are, in themselves, consistent with the initial hypothesis. The effect in the suppressed condition on the course of rivalry itself indicates that there was a continuous monitoring

of (phenomenally) suppressed information. To this extent the subjects' reports are consistent with the behaviour of the earlier components, in indicating that the (cortical) discrimination of visual material continues despite the phenomenal suppression that occurs in rivalry.

A recently-reported study, that is not complicated by the perceptual effects of the evoking stimulus, provides results that are consistent with these findings. Harter, Seiple and Salmon (1973) studied binocular interaction as it is reflected in the evoked response. They presented obliquely oriented line patterns, with varying degrees of contour density, to the two eyes. The patterns were either similarly oriented (dioptic condition) or oriented at right angles to each other (dichoptic condition). Both patterns were continuously back-illuminated in the steroscope. Additional flashes, 10μsec duration, were generated once every 1.5 sec, illuminating either one (monocular condition) or both (binocular condition) of the fields. Subjects indicated which of the fields they saw illuminated by each light flash. Three components of the evoked potential were identified that were comparable to those identified in the rivalry experiment. Whilst the first two were negative in polarity, with latencies to peak of 110 and 155 msec, the third was positive, with a latency of 210 msec.

On the basis of the rivalry experiment, the following would be expected: (i) the earlier negative components would not show any signs of interaction between the two monocular systems in either of the binocular conditions; rather these components would be expected to show enhancement, reflecting the summation of the two monocular responses: (ii) the behaviour of the late component should reflect the suppression of one of the two fields when this occurs, ie, in the dichoptic conditions that involve the patterns of greatest contour density.

Harter's results confirm these expectations. For both the dioptic and dichoptic conditions there was an enhancement of the early components. This enhancement was independent of the size of the pattern elements, and therefore independent of the phenomenal suppression of one of the fields. The later component showed a similar enhancement only in the dioptic condition. Moreoever, the non-

enhancement of this later component was shown to be correlated with the probability that the subject reported the suppression of one of the stimuli. Thus, the degree to which the late component was similar under the monocular and dichoptic conditions was correlated with the probability that only one of the two fields was perceived to have been flash-illuminated. This finding further reinforces the association between the late components and perceptual experience.

Whilst it may appear rather arbitrary that the 'size' of a component should reflect the degree to which the subject perceives just one of the two stimuli, a possible interpretation is that the population of cells whose 'late' activity is synchronized or 'time-locked' to the stimulus is much greater in the condition where both monocular stimuli are seen (cf Thompson and Bettinger, 1970).

We see from this study that when a paradigm is employed that is not complicated by the immediate reappearance of a dichoptically-suppressed stimulus to which an evoked potential is recorded (as was the case in Experiment 4) the presence of the late components is indeed correlated with perceptual dominance. This helps confirm the belief that the longer latency components observed in the suppressed condition of Experiment 4 were correlated with the almost immediate perceptual effects of the reversal of the suppressed grating. Moreover, Harter refers to studies by White and Bonelli (1970) and Spekreijse et al (1972) which obtained corresponding changes in the late component (P210) as a function of monocular and binocular viewing conditions. Unfortunately, earlier components of the potential were not specifically measured in these studies. A report by Kawasaki, Hirose, Jacobson and Cordella (1970), again referred to by Harter, also indicates that the late positive component (P200-250) is suppressed in response to dichoptic stimulation.

Clearly preferring the passive approach toward rivalry, Harter et al (1973) suggest that the late component (P210) reflects the activity of binocularly-driven cortical units, and that its behaviour in the dichoptic condition arises from the fact that these units are most effectively stimulated by similar stimuli when these are presented to corresponding retinal areas. However, evidence will be presented

later that militates against assigning such a role to binocularly-driven units and, moreover, there is evidence that the later components of the evoked potential reflect activity arising in structures other than primary visual cortex (cf below). In addition, having given this interpretation of the later components, Harter et al (1973) were obliged to suggest that the early components reflected the activity of first-order neurones from lateral geniculate. This suggestion is at odds with much other data (cf below, and Regan, 1972; MacKay and Jeffreys; 1973).

3.9.1 Conclusion

The present experiments, and those that have been reviewed, show that the late and not the early components of the transient evoked potential are the physiological indices of the phenomenal suppression in rivalry. Since the former have been associated with 'active' or endogenous processes (cf below), and the latter with discriminatory processes, the active approach toward rivalry receives good support.

In the next chapter more is made of these physiological indices, which, when consideration is given to the structures that contribute to their generation, suggest a physiological context for binocular rivalry and, more generally, for perception and attention. Before this, however, two experiments will be reported which focus on the perceptual effects of the complete reversal (cf Experiment 4) and the lateral displacement (cf Experiment 6) of the vertical grating. In the first experiment, subjects' introspective reports of the almost immediate reappearance of the vertical grating in the suppressed condition of Experiments 4 and 6 were confirmed. In the second experiment an attempt was made to determine whether the perceptual suppression in rivalry reflects processes of adaptation or habituation.

3.10 EXPERIMENT 7 THE PERCEPTUAL EFFECTS OF 'SHIFTING' A RIVALLING STIMULUS

In the suppressed condition of the evoked potential experiment, though the subjects reported that the vertical grating reappeared almost immediately it had disappeared, they did not see the pattern reversal that was the cause of this. In view of the fact that the evoked potential to the pattern reversal in this condition unexpectedly possessed late components, these introspective reports were particularly important. It was suggested, then, that these components reflected the immediate perceptual effect of the pattern reversal, and more will be made of this association in a later section. However, since the durations of the rivalry phases were not recorded, there was no way of checking subjects' introspective reports. The present experiment, therefore, attempted to fill this gap by focusing on the perceptual alternations themselves under the conditions of the evoked potential study. The same apparatus and stimuli were used in this as in Experiment 4, though the physiological recording equipment was not utilized.

An equally-important reason for undertaking this experiment was the fact that these immediate perceptual effects of the pattern reversal, if confirmed, would offer a most convincing demonstration of subliminal perception and, more specifically, of the continuous monitoring of a stimulus during its non-dominant phases.

3.10.1 (a) Complete reversal of the vertical grating

There were three conditions of stimulus presentation. Two of these, the suppressed and dominant conditions, were as in Experiment 4. In the former condition the reversal of the vertical grating was instigated immediately the subject reported this grating to be suppressed, and in the latter condition the reversal occurred immediately this grating was reported to be dominant. In the remaining (normal) condition, the rivalry was allowed to progress normally, so that neither pressing nor releasing the key caused any change in the vertical grating.

Each subject first undertook one trial under each of these three conditions. An equal number of subjects undertook them in each of the six possible orders of presentation and then repeated these first three trials in the reverse order.

From the data recorded on each trial, the mean dominance times for the vertical and horizontal gratings could be determined.

Subjects

Twelve subjects took part in the experiment. All were undergraduate students, four being first-year students in psychology.

Procedure

The subject first familiarized himself with the synoptophore, the rivalry between the two gratings, and the use of the key to report the course of the alternations. The six experimental trials followed, each lasting 90 sec, with a 1-minute rest-period between each. During this period the subject was encouraged to make whatever comments he wished about the preceding trial.

	First Presentation			Second Presentation		
	C_1	C_2	C_3	C_1	C_2	C_3
Mean dominance time of horizontal grating	2.27	2.06	0.94	2.27	2.37	1.00
Mean dominance time of vertical grating	4.56	5.27	4.89	5.59	5.49	5.17

Average values for the mean dominance times of the two gratings (in secs.).

C_1, C_2 and C_3 signify the normal, dominant and suppressed conditions respectively.

Table-20

Source	D.F.	S.S.	S.S.
Between subjects	11	16.41	221.50
Order	5	4.29	87.35
Between subjects within groups (Error)	6	12.12	134.15
Within subjects	60	46.65	159.55
C	2	25.22	1.72
C x Order	10	3.58	40.02
C x Error	12	1.52	11.698
P	1	0.19	4.65
P x Order	5	4.86	21.54
P x Error	6	4.04	34.20
P x C	2	0.21	2.39
P x C x Order	10	2.39	17.36
P x C x Error	12	4.64	25.98
Total	71	63.07	381.05

Results of analyses of variance on the mean dominance times of the horizontal (first column) and vertical grating (second column). "Order" refers to the order in which the conditions were undertaken. "C" refers to the condition of stimulus presentation, viz normal, dominant or suppressed.

"P" refers to the first versus second presentation factor.

Table 21

RESULTS AND ANALYSIS

All subjects indicated, quite unambiguously, that whilst they were aware of the pattern reversal in the dominant condition, they did not see any change in the vertical grating in the suppressed condition. Subjects simply confirmed the reports of the subjects in the evoked potential study, that this grating reappeared very quickly after disappearing.

Presented in Table 20 are the values, averaged over subjects and order of presentation, for the mean dominance times of each field, for each of the six trials. Presented in Table 21 are the ANOVAR tables for the two parameters. It is clear from these that there was no significant difference, involving the mean dominance time of either field, between the normal and dominant conditions. In contrast, though there was no change in the mean dominance time of the vertical grating in the suppressed condition, there was a significant reduction in the mean dominance time of the horizontal grating ($F = 60.39$; $df = 1,12$; $P < 0.005$), which was reduced from the value of 2.27 sec, obtained in the normal condition, to 0.97 sec.

It is clear from the results that in the previous evoked potential studies, subjects were reliable when reporting the immediate reappearance of the vertical grating in the suppressed condition. It is also clear from the mean values listed in Table 20 that this reappearance occurred within 1 sec of the pattern reversal.

Finally, it is interesting that if one were to assume that the pattern reversal at the beginning of a rivalry phase adds to the stimulus strength of the field concerned, then the data fall in line with the literal interpretation of Levelt's thesis.

3.10.2 (b) Lateral displacement of the vertical grating

A further six subjects completed the same experiment under the control conditions of Experiment 6, ie with the two vertical gratings within the left field of the synoptophore positioned so that a switch in illumination caused a slight lateral displacement of the vertical grating, rather than a complete 180 deg reversal in contrast.

RESULTS AND ANALYSIS

Presented in Table 22 are the values, averaged over subjects, for the mean dominance times of each field, under each condition. In Table 23 are the corresponding ANOVAR tables.

The effects of the lateral displacement were comparable to those arising from the complete reversal. There was no significant difference, involving the mean dominance time of either field, between the normal and dominant conditions. In contrast, whilst there was no change in the mean dominance time of the vertical grating in the suppressed condition, there was a significant reduction in the mean dominance time of the horizontal grating ($F = 9.48$; $df = 1,10$; $P < 0.025$), from 2.65 sec in the normal condition, to 1.11 sec in the suppressed condition. According to these results therefore, the perceptual effects induced by the pattern reversal in the preceding experiment and Experiment 4 seem not to be a result of areal changes in luminance, but a result of the changes in structure.

	First Presentation			Second Presentation		
	C_1	C_2	C_3	C_1	C_2	C_3
Mean dominance time of horizontal grating	2.03	1.94	1.02	3.27	2.68	1.20
Mean dominance time of vertical grating	3.24	2.96	2.96	2.27	3.16	2.84

Average values for the mean dominance times of the two gratings (in secs.) cf. Table 20 for code.

Table 22

SOURCE	D.F.	S.S.	S.S.
Between subjects	5	77.41	11.85
Within subjects	30	72.22	21.09
C	2	15.68	0.57
C x subjects	10	14.97	6.71
P	1	4.67	0.79
P x subjects	5	24.19	1.30
C x P	2	1.68	3.60
C x P x subjects	10	11.03	8.13
Total	35	149.63	32.94

Results of analyses of variance on the mean dominance times of the horizontal (first column) and vertical (second column) grating. cf. Table 21 for code.

Table 23

DISCUSSION

These two experiments confirm the introspective reports of the subjects in the evoked potential studies. Thus, when the vertical grating is either reversed or displaced at the beginning of its suppressed phases, it reappears very quickly; the mean duration of these phases being reduced from a normal value of approximately 2.5 sec to a value around 1 second. Confirmation of these reports not only adds something to the credibility of the explanation of the presence of the late components in the suppressed conditions of Experiments 4 and 6, but provides a most convincing demonstration of the continuous monitoring of non-dominant information and, therefore, of subliminal perception.

3.11 EXPERIMENT 8 ADAPTATION OR HABITUATION AS THE BASIS OF PERCEPTUAL SUPPRESSION IN RIVALRY

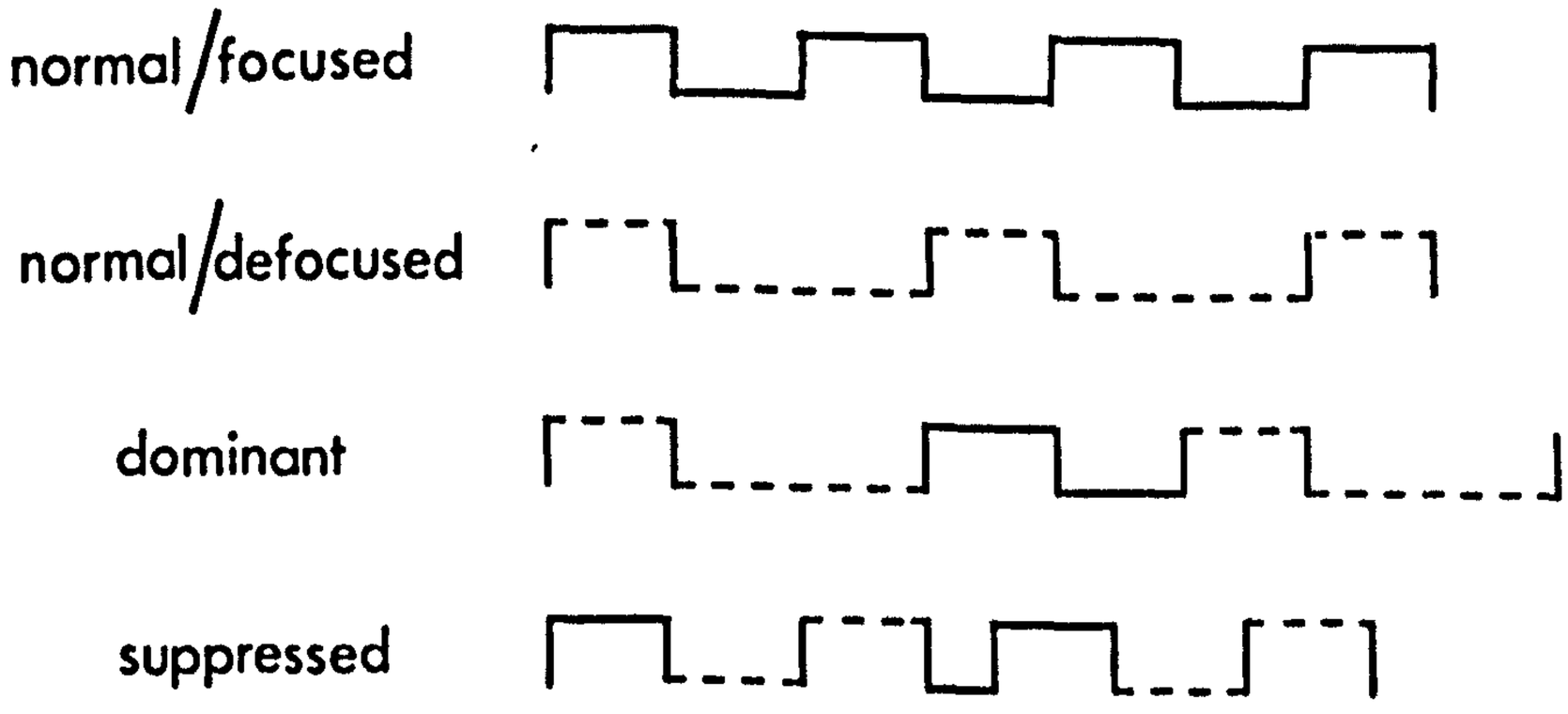
The fact that, as the preceding experiments demonstrate, the non-dominant stimulus continues to be monitored and fully analyzed discourages us from considering that the perceptual suppression in rivalry reflects underlying processes of adaptation. In view of the sensitivity to novelty of the mechanism responsible for monitoring non-dominant information (cf Experiment 3) and the identification of this mechanism with the physiological structures that readily display habituation (Chapter 4), an obvious alternative explanation may incorporate the notion of habituation. Indeed, such an explanation accords with the theoretical notions to be developed in a later chapter.

In arguing that habituation is distinct from adaptation in that it does not reflect a decrease in sensitivity, Sokolov (1960) made much of the fact that, when once habituated to the presentation of a tone signal, the orienting response could be reinstated by reducing the intensity of the tone. To provide a preliminary test of a habituation, rather than an adaptation explanation of the suppression in rivalry, an experiment was undertaken that incorporated these same principles. Thus, it was asked if reducing the 'stimulus strength' (Levelt, 1966) of a rivalling field during its suppressed phases would cause a shift in perceptual dominance in the same way that pattern reversal does.

Perhaps the most obvious way to test this would be to adopt the paradigm and stimuli of Experiment 7 and employ a change from a vertical grating in focus to an identical grating out of focus, instead of the pattern reversal previously used. This, of course, would allow a literal interpretation of Levelt's thesis to be tested using a parameter that he employed in his original studies, and around which he defined 'stimulus strength'. However, this procedure would also involve re-focusing the vertical grating, perhaps during its dominant phase, and so would allow for a confounding of effects. In order to circumvent this problem a rather cumbersome design was employed which permitted a less stringent test of the literal interpretation of Levelt's thesis.

Figure 17

Imaginary chart records illustrating the course of the alternations between the two gratings under the different conditions of experiment 8. Upward deflection of the records signifies dominance of the vertical grating, and downward deflection dominance of the horizontal grating. The dashed sections of the records signify periods in which the vertical grating is de-focused. Using just three possibilities for the duration of dominance of each field, the records are drawn in a way that summarizes the results of the study.


normal/focused
normal/defocused
dominant
suppressed

METHOD

Represented in Fig 17 are the different conditions of the experiment. The records plot the imaginary course of alternations between the two gratings previously used. In the two normal conditions there was no contingency arranged between the subject's report of the currently-dominant stimulus, and whether the smaller, vertical grating was in or out of focus. In the normal/focused condition both gratings were in focus and allowed to rival without interruption. The same held for the normal/de-focused condition except that the smaller grating was now continuously out of focus.

In the dominant and suppressed conditions a contingency was arranged between the subject's report of the rivalry alternations and the conditions of the vertical grating. In the dominant condition, each time the subject reported the vertical grating to have re-gained dominance its character was changed, either from being focused to being de-focused, or vice versa. In the suppressed condition the same changes were initiated each time the subject reported that the vertical grating had become suppressed. The dotted sections of the records signify periods in which the vertical grating was de-focused.

Each subject first undertook one trial under each of the four conditions, in an order that was randomly determined. These first four trials were then repeated in reverse order.

APPARATUS

Modification to the basic set-up involved one of the two vertical gratings that were situated in the left field of the synoptophore. Thus, on the front surface of one of these gratings was placed a thin semi-transparent sheet of plastic. As a result of this rather crude procedure (it is not known which of the spatial frequencies that make up the original square wave modulation are filtered out), the grating appeared considerably blurred. The space averaged luminance of the other vertical grating was adjusted to match that of the modified grating and their relative positioning within the left field of the

synoptophore was such that they were 'in phase'. Switching illumination from one vertical grating to the other thus had the effect of focusing or de-focusing the image.

SUBJECTS

Twelve subjects took part in the experiment. All were undergraduate students, though none were psychologists.

PROCEDURE

Each trial lasted 60 sec, with a 1-minute rest-period allowed between each. During this period the subject was encouraged to make whatever comments he wished about the preceding trial, prompted by the question "Was that any different from previous trials, and in what way?"

	a	b
normal/focused	6.25	1.54
normal/defocused	5.36	2.06
dominant/focused	6.05	1.71
dominant/defocused	5.91	2.13
suppressed/focused	6.24	0.80
suppressed/defocused	4.80	1.14

Average values for the mean dominance times of the vertical, (a), and horizontal, (b), gratings under the different conditions of experiment 8 (cf. Fig. 17).

Table 24

SOURCE	D.F.	S.S.	S.S.
Between subjects	7	56.61	323.59
Within subjects	88	74.44	619.66
C	5	21.46	26.37
C x subjects	35	20.51	255.19
P	1	0.21	31.29
P x subjects	7	6.46	44.81
C x P	5	4.97	54.97
C x P x subjects	35	20.84	207.05
Total	95	131.05	943.25

Results of analyses of variance on the mean dominance times of the horizontal (first column) and vertical (second column) gratings.

"C" refers to the conditions of stimulus presentation, viz. normal/focused, normal/defocused, etc.

"P" refers to the first versus second presentation factor.

Table 25

RESULTS AND ANALYSIS.

Regarding the dominant and suppressed conditions, the dominance times for the two fields that emerged from periods when the vertical grating was in focus were treated separately from those emerging from periods when it was out of focus. The results from these two conditions were, therefore, sub-divided on the basis of this distinction. The average values obtained for the mean dominance time of the two fields are given in Table 24, where the distinction between first and second presentation is ignored. The summary ANOVAR tables are presented in Table 25.

A comparison of the results from the two normal conditions shows a consistency with Levelt's (1966) findings and supports his thesis. Thus, whilst de-focusing the vertical grating clearly did not change the mean duration for which it was dominant ($F = 0.876$; $df = 1,35$; $P < 0.05$), it did cause the mean duration of dominance of the contralateral field to be increased ($F = 3.654$; $df = 1,35$; $P < 0.05$), though this just failed to be significant. A comparison of the results from the dominant and suppressed conditions with those from the normal condition allows one to determine if a change in the status of the vertical grating, initiated at the beginning of one of its dominant or suppressed phases, significantly alters the course of rivalry. Tests failed to reveal a significant difference between either the normal/focused and dominant/focused, or the normal/de-focused and dominant/de-focused conditions, with reference to either the mean duration of dominance of the vertical grating ($F = 0.043$; $df = 1,35$; $P < 0.05$ and $F = 0.339$; $df = 1,35$; $P < 0.05$) or the horizontal grating ($F = 0.353$; $df = 1,35$; $P < 0.05$ and $F = 0.056$; $df = 1,35$; $P < 0.05$). Thus, changing the vertical grating at the beginning of one of its dominant phases did not alter the course of rivalry.

The same comparisons between the suppressed and normal conditions did reveal significant effects however. Thus, contrasting the suppressed/focused and normal/focused conditions revealed a significant reduction, in the former condition, of the mean duration of dominance of the horizontal grating ($F = 7.63$; $df = 1,35$; $P < 0.01$) but no similar difference involving the mean duration of dominance

of the vertical grating itself ($F = 0.001$; $df = 1,35$; $P < 0.05$). Similarly, contrasting the suppressed/de-focused and normal/de-focused conditions revealed a significant reduction, again in the former condition, of the mean duration of dominance of the horizontal grating ($F = 11.537$; $df = 1,35$; $P < 0.005$) and again no similar difference involving the mean duration of dominance of the vertical grating itself ($F = 0.332$; $df = 1,35$; $P < 0.05$).

To summarize, therefore, changing the character of the vertical grating, in a way that either increases or decreases its stimulus strength, induces a reduction in the duration for which the field remains non-dominant. Consistent with the results of the previous studies, and with Levelt's thesis, there were no changes in the mean duration of dominance of the vertical grating. Furthermore, the fact that there were no changes in the mean duration of dominance of either field as a result of changing the vertical grating at the beginning of its dominant phases is consistent with the literal interpretation of Levelt's thesis.

Contrasting the dominant/focused and suppressed/focused against the dominant/de-focused and suppressed/de-focused conditions provides a test of the literal interpretation of Levelt's thesis, where stimulus strength is varied according to whether the vertical grating is in or out of focus (not whether it changes status as above). Supporting the literal interpretation was an increase in the mean duration of dominance of the horizontal grating when the vertical grating was de-focused ($F = 4.0119$; $df = 1,35$; which just fails significance at the 5% level), with no comparable change in the mean duration of dominance of the vertical grating ($F = 1.35$; $df = 1,35$; $P < 0.05$). Considering the suppressed condition alone, or the dominant condition alone, there is a confounding of effects due to the state of the vertical grating whilst it is suppressed (or dominant) and to the conditions of the preceding phase (for example, in the dominant condition a suppressed phase of the de-focused vertical grating is always immediately preceded by a dominance phase during which it is also de-focused, whilst a suppressed phase of the focused vertical grating is always immediately preceded by a dominance phase during which it is also focused). However, the fact

that the results in the two conditions are in the same direction suggests that this is not an important factor, since it would encourage opposite results in the two conditions.

DISCUSSION

When the vertical grating was de-focused for the total duration of a trial, the effects on the course of rivalry confirmed Levelt's (1966) original observations and hence supported his thesis. Thus, whilst de-focusing this grating did not significantly change the mean duration for which it was dominant, it did cause the mean duration for which it was non-dominant to be significantly increased. Moreover, when, within the same trial, the vertical grating was alternately focused and de-focused for its dominant or non-dominant phases, though the design possibly confounded two factors, the results supported the literal interpretation of Levelt's thesis. Thus, the 'strength' of the vertical grating (whether it was focused) influenced the course of rivalry only whilst it was non-dominant.

In respect of the aim of the experiment, the important finding was that changing the status of the vertical grating at the beginning of its suppressed phases influenced the course of rivalry even when this change involved de-focusing the grating and hence a reduction in its strength. This finding suggests that the perceptual suppression in rivalry is more likely to reflect processes of habituation than adaptation. Moreover, the fact that the effects of changing the stimulus in this way were restricted to a reduction of the mean duration of the vertical grating's suppressed phases, and that no comparable effects were obtained when the grating was changed at the beginning of its dominant phases, confirms yet again the literal interpretation of Levelt's thesis.

Finally, it needs to be discussed why decreasing the stimulus strength (de-focusing the vertical grating), when this occurs during a suppressed phase of the field involved, should have the same effect on the course of rivalry as increasing the stimulus strength. It would appear from this and the preceding two experiments that Levelt's definition of stimulus strength must be extended to incorporate aspects of the stimulus other than its physical structure. Change per se, or selective information content, appears to be a contributor to the strength of a stimulus. We have already seen evidence for this in Experiment 3.

PART 2

A THEORETICAL FRAMEWORK FOR BINOCULAR RIVALRY: THE PHYSIOLOGICAL BASES OF PERCEPTION AND ATTENTION

CHAPTER 4 A PHYSIOLOGICAL CONTEXT FOR BINOCULAR RIVALRY

It may be asked whether the changes in the late components of the evoked potential that accompany rivalry suppression are consistent with other data. Should these changes have been anticipated, and what do they reveal about the nature of binocular rivalry?

4.1 The Distinction Between the Early and Late Components of the Evoked Potential

In order to better understand the implications of the evoked potential changes that correlate with rivalry suppression, the significance of the late components themselves needs to be discussed. Since there is some doubt as to the validity and usefulness of the distinction between early and late components (cf. Tecce, 1970) some basic findings need to be summarized:

1. The different components have different topographical distributions over the scalp (Kooi and Bagchi, 1964; Satterfield, 1965; Spong, Haider and Lindsley, 1965; Pagni, 1967; Vaughan and Ritter, 1970; Garcia-Austt and Buno, 1969) suggesting that distinct physiological mechanisms are involved in their generation.
2. Whilst the behaviour of the early components correlates particularly well with the intensity and other physical parameters of a stimulus, this is generally not the case for the later components (cf. Donchin, Kubovy et al, 1973; Jeffreys, 1969; Ritter, Simson and Vaughan, 1972; Regan, 1972). In contrast, evoked potential correlates of "meaning", or stimulus significance, are to be found primarily with the later components (John et al, 1967; Begleiter et al, 1967; 1969).

3. The latencies of only the later components covary with reaction time (Ritter, Simson and Vaughan, 1972; Garcia-Austt and Buno, 1969).

4. Habituation procedures have rather selective effects on evoked potentials, primarily affecting the later components (Brazier, 1964; Pagni, 1967).

5. Early and late components have markedly different recovery functions (Allison, 1962). Thus, the times to full recovery for the early and late components have been found to be 300 msec. and 4 sec. respectively (Allison, 1962).

6. A late positive component may occur in the absence of any early components. Evoked, or "emitted" potential as they are known (Weinberg et al, 1970), may be observed in the EEG in response to the non-occurrence of an expected event, and these consist essentially of a late positive component (Haider, 1970; Ruchkin and Sutton, 1973; Sutton, Tueting, Zubin and John, 1967; Garcia-Austt and Buno, 1969).

7. Finally, operant conditioning techniques have proved successful in selectively modifying the amplitude of a late component, in cat (Fox and Rudell, 1970) and in man (Rosenfeld, Rudell and Fox, 1969).

Additional findings could be cited in support of the distinction between early and late components, and indeed, data that are to be discussed in the following sections have just such a bearing on the problem.

Accepting the distinction, it may be asked whether the behaviour of the late components in rivalry is consistent with the psychological processes with which they have been correlated. How have the late components been interpreted, and are these interpretations consistent with their behaviour in binocular rivalry? That the later components not only correlate with perceptual experience, but reflect "active", or endogenous processes is evident from several areas of research. Furthermore, consistent with the notion that binocular rivalry reflects attentional processes (cf. Chapter 2) the later component, P300, has been identified with attention and orientation.

4.1.1 Late components and perceptual experience

Consistent with their behaviour in rivalry, the late components have been associated with conscious perceptual experience. Reference will later be made to the neurophysiological evidence provided by Goff (1969) that links the early and late components with activity in the lemniscal and extralemniscal systems respectively. Observing that late components are altered or absent under conditions in which perceptual awareness is altered or absent, Goff correlates these components with perceptual experience. Thus, human late responses were shown to be particularly sensitive to pentathol anaesthesia (Abrahamian, Allison, Goff and Rosner, 1963) and as consciousness was lost, so the late components were obliterated. This contrasted with the behaviour of the early components which were unaffected or even potentiated by the anaesthetic, even to the point where the patient was ready for surgery. More direct demonstration of the association between the late components and conscious perceptual experience has been reported by Libet (cf. Libet, 1973 for a review). With subdural electrodes on postcentral

gyrus, evoked potentials were recorded to stimulation of skin and ventroposterolateral nucleus of the thalamus that was well below the subjects conscious sensory threshold (Libet et al, 1967). It was discovered that these potentials consisted of the early components only. The late components appeared around the conscious sensory threshold level, the point at which the subject was uncertain about whether he felt the stimulus. Libet also observed that the perception of a peripheral stimulus could be masked by direct stimulation of the somatosensory cortex when this interfered with the later components of the cortical response. Similarly, Lindsley and Emmons (1958) have reported that a masking stimulus presented within 50 msec. of a signal both blocks the later components of the evoked response and prevents the conscious perception of the signal.

From this, it is understandable that the late components, unlike the early components, should have been absent from the evoked potential to a suppressed stimulus in binocular rivalry.

4.1.2 Late components and endogenous processes

In the context of the active approach toward rivalry, the evidence which links the later components with active, or endogenous processes is particularly consistent with their behaviour in rivalry.

E.R.John et al (1973) demonstrated that the waveshape of the evoked potential to a stimulus need not be solely determined by its physical properties, but rather may reflect the activation of endogenous neural processes. Thus, though the presentation of an ambiguous stimulus elicited varying waveshapes, on each occasion the waveshape

corresponded to that normally elicited by the conditioned stimulus appropriate to the behaviour performed. Thus, when a cat performed two different responses to the presentation of the same stimulus, two different waveshapes were obtained. One reproduced the waveshape usually elicited by the conditioned stimulus for one behaviour, whilst the other reproduced the waveshape associated with the discriminative stimulus for the other behaviour. The difference in waveshape that correlated with the behavioural response were almost exclusively confined to the late components. John et al (1973) concluded that these components reflect "the cognitive decisions about the significance or meaning of an afferent input" (p. 921). As we shall see, others have given a similar interpretation to the behaviour of a specific late component, P300.

The clearest demonstration of the endogenous nature of the processes underlying the later components comes from studies of emitted potentials. Thus, when an expected event (stimulus) does not occur the components of an evoked potential appear at latencies similar to the late components of potentials evoked by the occurrence of expected stimuli. Such emitted potentials have been recorded by Barlow, Morrell and Morrell (1967), Barlow (1969), Klinke et al (1968), Rusinov (1959), Sutton et al (1967), Haider (1970), Weinberg et al (1970; 1974), Picton et al (1973), Garcia-Austt and Buno (1969) and Ruchkin and Sutton (1973).

In conclusion, since the second approach towards rivalry holds that an active process is the basis of perceptual experience, and more specifically is the basis of the dominance in rivalry, the association between the late components, endogenous psychological processes and conscious perceptual experience is consistent with their behaviour in rivalry.

Investigations of the psychological significance of a particular late component help to more precisely define the active process that is the basis of perceptual dominance. It is suggested that the process is related to the matching of sensory data against a neuronal model, which in turn is an internal component of the orienting response. This is consistent with the results of the binocular rivalry experiment. These investigations relate to the late positive component, of 250-500 msec. latency, known as P300.

4.1.3 The interpretation of P300

Although the return to baseline of the Contingent Negative Variation (CNV) may have been mistakenly identified as a late positive component of the evoked potential (i.e. P300) in a number of early studies (cf. Naatanen, 1969; 1970), these two responses have since been dissociated (Donald and Goff, 1971; Tueting and Sutton, 1973; Walter, 1969), indicating that there is a P300 component that requires interpretation.

Though there are currently many different interpretations* these are not always incompatible, and indeed, a single

* The most popular interpretations of P300 are that it reflects: arousal or activation (Eason, Aiken et al, 1964; Jane, Smirnov and Jasper, 1962); attention (Donchin and Cohen, 1967; Haider, Spong and Lindsley, 1964; Satterfield and Cheatum, 1964; Satterfield, 1965; Spong, Haider and Lindsley, 1965; Corby and Kopell, 1973); information delivery/uncertainty resolution (Donchin and Cohen, 1967; Klinke et al, 1968; Picton and Low, 1971; Sutton, Braren, Zubin and John, 1965; Sutton, Teuting,Zubin and John, 1967 a,b; Tueting, Sutton and Zubin, 1971); response readiness (Peters et al, 1970); internal matching/evaluation of sensory information (Ritter and Vaughan, 1969; Klinke et al, 1968); decision processes (Davis, 1964; Shelbourne, 1972; Smith, Donchin, Cohen and Starr, 1970); Stimulus/task relevance (Chapman and Bragdon, 1964; Chapman, 1969; Donald and Goff, 1971; Smith et al, 1970; Sutton et al, 1970).

interpretation may accommodate the available evidence.

Ritter, Vaughan and Costa (1968) argue that P300 reflects the central or internal components of the orientation response, and additional evidence may be recruited in support of this. Thus, a stimulus that entails a degree of novelty, incongruity, complexity or uncertainty not only initiates an orientation response (cf. Berlyne, 1960; Lynn, 1966) it also induces, or augments the P300 component (Donchin et al, 1973; Klinke et al, 1968; Sutton, Braren, Zubin and John, 1965; Ritter, Simson and Vaughan, 1972; Roth, 1973; Tueting, Sutton and Zubin, 1971; Ruchkin and Sutton, 1973). For example, Haider (1970) has discovered that the later components are greater for a stimulus that occurs 370 msec. earlier than expected than for one occuring only 200 msec. too early. Indeed, Ritter et al (1968) have demonstrated the equivalent of dishabituation with respect to the P300. Thought to be difficult to reconcile with the orientation-response interpretation is the fact that P300 is enhanced (i) when the subject is required to attend, discriminate or perform a simple reaction time task to the stimulus (Donchin and Cohen, 1967; Haider, Spong and Lindsley, 1964; Satterfield, and Cheatum, 1964; Satterfield, 1965; Spong, Haider and Lindsley, 1965; Corby and Kopell, 1973; Davis, 1964; Harter and Salmon, 1972; Donchin, Kubovy, Kutas, Johnson and Herning, 1973), and (ii) when stimuli are presented at a near threshold level (Donchin, 1968). Thus, both predictable and unpredictable stimuli elicit a P300 when a reaction time demand is imposed on the subject. This is, however, consistent with an orienting reaction interpretation since the components of this reaction may appear and/or be made more resistant to habituation under these very same conditions (cf. Lynn, 1966). Nevertheless, there are

a number of component processes to the orienting response, and it is difficult to determine which of these is critical in generating P300. In line with Sokolov's (1960) model, Ritter and Vaughan (1969) envisage that incoming sensory information is matched against a neuronal model and that the results of this matching process are then evaluated, to determine whether the mismatch that occurs is sufficient to warrant a change in the model. Different component processes have already been associated with P300, viz. the degree of mismatch (Klinke et al, 1968; Tueting, Sutton and Zubin, 1971), the "goodness" of the template match (Squires, Hillyard and Lindsay, 1973), and the evaluation of the mismatch signal (Ritter et al, 1969; John et al, 1973). Whilst there is agreement as to the orienting nature of the processes underlying P300, the fine detail of the psychological significance of P300 remains to be determined.

To anticipate the content of a later chapter, it may be suggested that most consistent with the experimental evidence, is the notion that it is the successful matching of a model that correlates with the presence of P300, and thereby with perceptual experience. It is not the degree of mismatch, nor its evaluation, since, as we have already seen, P300 may be observed in response to a predictable stimulus. Consistent with this suggestion that P300 reflects the successful matching of a model, evidence will be discussed in a later chapter which indicates that the latency of P300 is increased when there is a greater mismatch between the incoming sensory information and the neuronal model. Clearly, whilst there is no reason for believing that the detection or evaluation of the mismatch should be delayed in such a situation, the successful matching of a model might clearly be delayed.

Insofar as we may assume that the late positive component labelled P300 is also a component of the evoked potentials observed in the binocular rivalry experiments, the implication of all this is that perceptual dominance in rivalry reflects the successful matching of sensory information with an internal neuronal model. To be consistent with this however, it needs to be assumed that the neuronal model should incorporate only the information originating in one eye, and furthermore, that the matching process should in some way avoid the sensory information originating in the other eye since this would serve to disconfirm such a restricted model; but more will be said of this later.

To conclude this section, the evidence relating to the psychological significance of the later components of the evoked potential suggest that it is the successful matching of sensory information against a neural model that underlies conscious perceptual experience. Consistent with the "active" approach to perception and attention, conscious perceptual experience is thus considered to be something over and above the discrimination and recognition of a stimulus.

4.1.4 Summary

To summarize, the data reviewed in the preceding sections indicate that what is known of the psychological correlates of the late components of the evoked potential is consistent with their behaviour in binocular rivalry. Thus, whilst these components have been correlated with conscious perceptual experience and attention, so they appear in response to the dominant, and not to the non-dominant stimulus in rivalry. Moreover, in line with the active approach toward rivalry, these late components have been associated with active, or endogenous psychological processes. Finally, consideration was given to research that has focused on the P300 component, and it was argued that the interpretation that best accommodates the wide variety of data is one which links this component with some internal aspect of the orienting reaction. This aspect was identified with a matching process whereby incoming sensory data is compared with an "hypothesis" or internal model. Whilst there are a number of aspects to this matching process, it was suggested that it is the confirmation of a model, a successful matching, with which the presence of P300 may be identified.

4.2 The Physiological Structures Contributing to the Late Components of the Cortical Evoked Potential

With the evoked potential serving as a bridging factor between physiological and psychological processes, we may next ask what physiological mechanisms might underly the active process that is the basis of perceptual dominance in rivalry, and more generally the basis of conscious perceptual experience and attention.

Experiments have pointed to a distinction between the brain structures that contribute to the different components of the evoked potential. Whilst the functional significance of the structure that is traditionally associated with the late components is particularly consistent with the evoked potential correlates of rivalry, more recent evidence, that implicates the midbrain-association cortex in the generation of these components, is in this respect somewhat paradoxical. This paradox, however, serves usefully to delineate the physiological processes underlying conscious perceptual experience and attention.

Frontal cortex

In view of the fact that the CNV may return to baseline approximately 300 msec. after presentation of the expected stimulus, it must be accepted that the frontal cortex may contribute a late positive component to the evoked potential (Karlin, 1970; Donchin and Smith, 1970; Donchin and Cohen, 1967; Naatanen, 1969; 1970; cf. also Donald and Goff, 1971; McAdam, 1969; Walter, 1964b). However, it seems unlikely that the CNV reflects any significant processing of sensory information (Posner et al, 1973) and moreover, as has already been mentioned, the P300 component may exist independently of a return to baseline of the CNV.

Reticular Activating System

Consistently implicated in the generation of the late components of the scalp evoked potential are structures other than primary visual cortex. Partly because of their sensitivity to barbiturate anaesthesia and sleep, these components have been associated with the reticular activating system (RAS) (Abrahamian, et al, 1963; Bergamini and Bergamasco, 1967; Uttal and Cook, 1964; Williamson, Goff and Allison, 1970; Goff, 1969; Steriade, Belekhova and Apostol, 1968; John, 1967; Begleiter and Platz, 1969). This contrasts with the earlier components which because of their relatively restricted distribution over the scalp and their insensitivity to barbiturates and sleep, have been associated with the primary cortical areas. More, specifically, it has been suggested (cf. for example, Goff, 1969) that the specific projecting, fast recovering, short latency evoked response components result from cortical activation by impulses travelling in the lemniscal afferent system, whilst the diffusely projecting, slower recovering components result from activity in the non-specific extra-lemniscal system.

Dixon's (1971) analysis of the physiological bases of subliminal perception highlights the association between the RAS and conscious perception. He suggests that whilst a subliminal stimulus is successfully signalled by the specific, lemniscal afferent system, and fully discriminated by the cortex, it does not recruit the necessary nonspecific activation from extra-lemniscal sources, particularly the RAS. It is this latter fact which, it is argued, is responsible for the stimulus' failure to register in consciousness.

Associating the late components with the reticular activating system on the one hand, and with perceptual dominance in rivalry on the other, suggests that the selective activation of restricted regions of the cortex may be the active process that underlies conscious perceptual experience and attention. As Livingston (1959) points out, "the possible interplay between the cortical discriminatory mechanism and the RAS, provides the perceptual process with an <u>active</u> principle that incorporates an element of purpose in its selectiveness" (p. 757). However, there is some question about whether it is sensory cortex that is the direct recipient of activation from the RAS, or association cortex. Though in his model of perceptual defence Dixon (1971) perhaps implies the former (cf. his Fig. 9.2), there are data which indicate that the latter is the case (cf. below), and that sensory cortex is influenced by the RAS via posterior association cortex. Though perhaps complicating the matter, this fact makes much more sense when we consider the possible contribution of association cortex and related structures to the late components of the evoked potential.

The hypothesized involvement of the RAS in the generation of the late components of the evoked potential is also consistent with the orientation-reaction interpretation of P300, since the most comprehensive model of the orientation reaction (Sokolov, 1960; Voronin and Sokolov, 1960) involves the following assumptions: (i) in addition to sensory

information being transmitted along the classical sensory tracts to the cortex, information is transmitted, via afferent collaterals, to the reticular formation;
(ii) in the case of a stimulus being identified as novel or significant, the cortex interacts with the RAS to initiate the orientation reaction, part of which involves RAS influence on the relevant cortical zones. Bearing in mind Dixon's delineation of the conditions necessary for subliminal perception, there would appear to be a correspondence between conscious perception and the orienting reaction. Thib is consistent with the association of P300 with both of these processes.

To conclude, the identification of the late components with the RAS is consistent with the changes in the evoked potential that accompany the suppression in binocular rivalry. In the same way that the early components may be gnerated in the absence of a phenomenal correlate, so it is that activity in the lemniscal system is not a sufficient condition for RAS involvement, or for awareness of a stimulus (Libet, 1967; 1973; Goff, 1969; Magoun, 1954; Moruzzi and Magoun, 1949; Samuels, 1959). In terms of the active approach toward rivalry the possible involvement of the RAS suggests that the activation of cortex is the active process that is the basis of perceptual dominance. However, more direct and compelling evidence that implicates the superior colliculus-association cortex system in the generation of the late components, suggests that the RAS may contribute only indirectly, via its close relationship with posterior association cortex, to the late components of the evoked potential and to the perceptual dominance of a stimulus.

Superior Colliculus and Association Cortex

Not incompatible with the involvement of the RAS, or with the orientation reaction interpretation of P300, is the evidence that the later components reflect activity arising in association areas of the cortex (Heath and Galbraith, 1966; Aoki, 1969; Vaughan, 1969b; Regan, 1972; Harter and Salmon, 1972; Vaughan and Ritter, 1970). This is consistent with the differing susceptibility of the early and late components to barbiturate anaesthesia and habituation (Buser and Bignall, 1967; Brazier, 1964; Pagni, 1967). Thus, activity arising in association cortex (in contrast to activity in primary cortex), like the later components, is susceptible to habituation (Walter, 1964b; 1965; Buser and Bignall, 1967; Thompson et al, 1969; 1970). Furthermore, gross activity in association cortex, again like the late components, is particularly well correlated with psychological factors, whilst gross activity in primary cortex, like the early components, is best correlated with the physical parameters of the stimulus (Walter, 1964; Buser and Bignall, 1967).

Gerbrandt, Spinelli and Pribram (1970) have provided more direct evidence for the involvement of association cortex in the generation of the later components. These authors recorded the striate evoked response to stimulation of the lateral geniculate body in rhesus monkey, and compared the effects of inferotemporal cortex stimulation with having the animal attend. As expected, it was the late components of the response that were increased considerably by having the monkey attend, but more importantly, inferotemporal cortex stimulation had the same effect.

It is understandable that there should be this degree of correspondence between the activities of association

cortex and RAS, since it is to association cortex and not to primary cortex that the latter projects, and from association cortex that the latter receives projections (Philips et al, 1972; French et al, 1955; Segunda et al, 1955; Buser and Bignall, 1967). Thus, the involvement of these two structures in the generation of the late components is not inconsistent.

Though it is only recently that the superior colliculus -association cortex system has been implicated in the generation of the late components of the visually evoked cortical potential, the evidence is more direct than that which implicates the RAS. Moreover, in view of the RAS' relationship with posterior association cortex, the evidence for its involvement is also not inconsistent with the significance of these other structures. Finally, the contribution of the superior colliculus-association cortex system to the generation of the later components is consistent with the orienting response interpretation of P300. In the previous discussion of this system it was concluded that it is involved in the orienting reaction (cf. chapter 3).

Rose and Lindsley (1968) studied the development of the visual evoked cortical potential in kittens, as recorded on the surface of the cortex. They discovered two separate and independent components that could be distinguished on the basis of age of appearance, polarity, latency, amplitude and cortical distribution. The long latency response could be recorded not only over primary visual cortical areas, but also over non-primary areas. In contrast, the short latency response could not be found over the outlying, non-primary areas, being confined mainly to visual areas I and II. The short latency response,

because of its restricted distribution, was taken to reflect activity in the specific sensory system, whilst the longer latency response was thought to reflect activity of the nonspecific system. Rose and Lindsley then hypothesized that the former response was mediated by the geniculo-striate projection, whilst the latter reflected mediation by the superior colliculus. They confirmed this by studying the effects of lesions in these different areas of the brain. Whilst lesions of the superior colliculus abolished the long latency response and did not affect the shorter latency response, lesions of the lateral geniculate had the opposite effect.

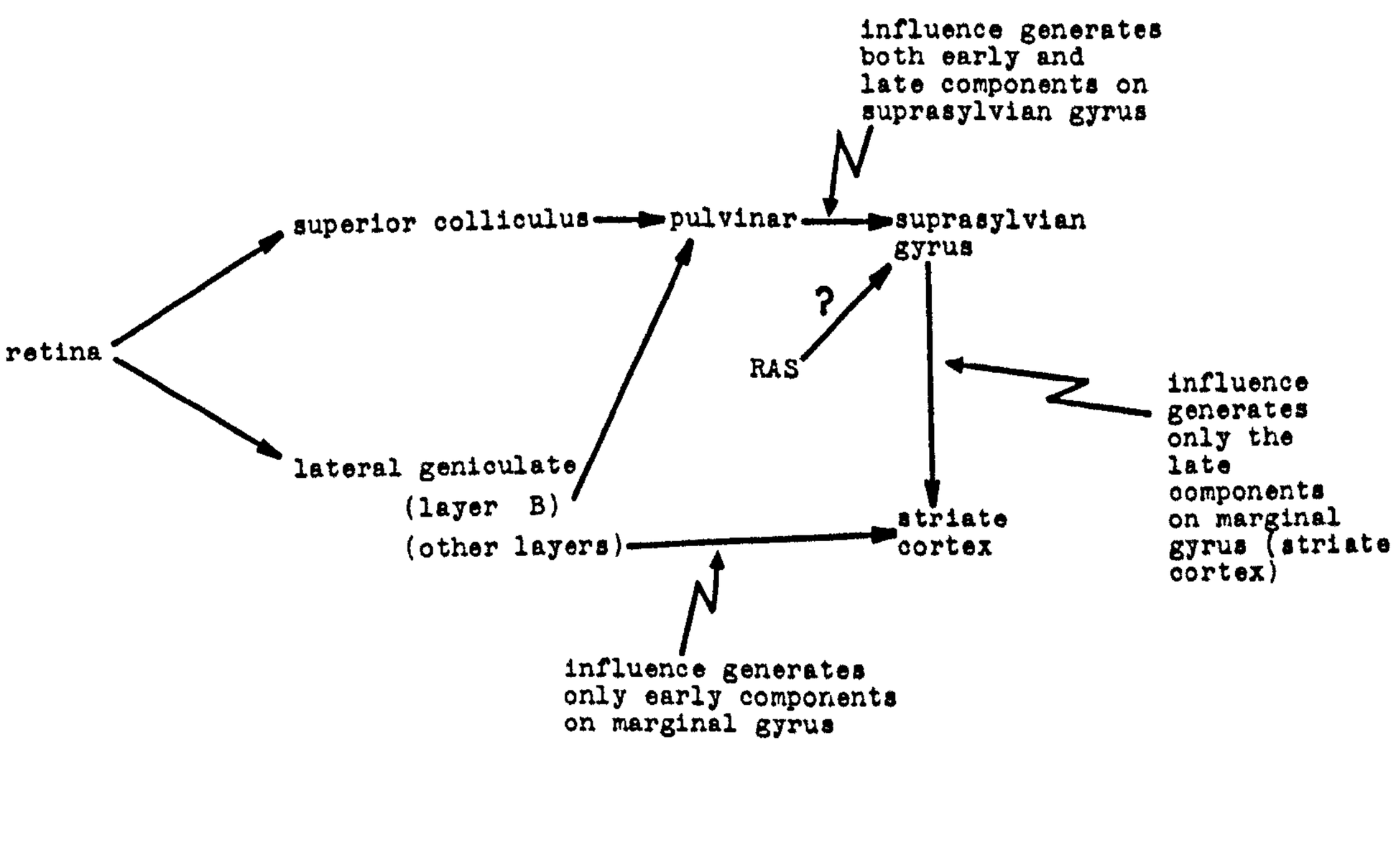
Chalupa, Anchel and Lindsley (1973) have recently studied the effects of cooling the pulvinar on the visually evoked cortical response of cat. They discovered that the visual evoked potentials on the suprasylvian gyrus and marginal gyri (visual cortex) were markedly diminished in amplitude by cooling the pulvinar. Responses recorded over both areas incorporated both early and late components, and whilst both components on the suprasylvian gyrus were reduced by pulvinar cooling, only the later components on the marginal gyrus were thus affected. By cooling the suprasylvian gyrus, the latter effect (and thus the later components under normal conditions) was shown to be mediated by this area of association cortex. Effects similar to those resulting from cooling the pulvinar were also shown to follow the cooling of layer B in the lateral geniculate (cf. Dow and Dubner above). It is known that in cat this layer provides visual input to the pulvinar. In contrast, cooling layer A, which projects directly to striate cortex, caused a reduction of only the primary response components on the marginal gyrus. These authors conclude, therefore, that there exist two visual inputs to cortex, one via the geniculo-striate pathway and another

via the pulvinar-suprasylvian gyrus pathway. Whilst the former is mainly responsible for the primary components of the evoked response recorded over visual cortex, the latter is responsible for the later components of this response. Chalupa et al further suggest, and this is consistent with the results of Gerbrandt et al, that since the later components of the evoked potential in humans have been associated with attention, so the pulvinar-suprasylvian gyrus complex may function in attention. This is entirely consistent with the thesis that is being developed.

Figure 18 summarizes what is known of the physiological structures that contribute to the generation of the evoked potential. With reference to this, two further points may be made. First, consistent with the proposed origin of the late components of the evoked potential, it has been shown that information in the peripheral visual field contributes mainly to these later components (Rietveld, 1966). Second, this recent neurophysiological evidence again confirms that the early components of the evoked potential, as recorded over visual cortex, reflect the latter's response to the stimulus.

Figure 18

Schematic representation of the structures responsible for the different components of the visual evoked potential in cat.


influence generates both early and late components on suprasylvian gyrus
superior colliculus
pulvinar
suprasylvian gyrus
retina
?
RAS
lateral geniculate
(layer B)
(other layers)
striate cortex
influence generates only the late components on marginal gyrus (striate cortex)
influence generates only early components on marginal gyrus

4.2.1 Summary

To summarize, it has been argued that a useful and valid distinction can be made between the early and late components of the evoked cortical potential, and that different psychological processes may be identified with their generation. Focusing on the late components, it was seen that their identification with "active", endogenous processes, and more importantly with conscious perceptual experience, is entirely consistent with the evoked potential correlates of binocular rivalry. With regard to the nature of the active process that is thought to underly perceptual experience, and more specifically the perceptual dominance in binocular rivalry, the research that has focused on a particular late component, P300, was interpreted to suggest that this process may be a matching process whereby incoming sensory information serves to confirm an internal model of the world.

In the last section, it was argued that the physiological structures most directly responsible for the generation of the late components may be identified, and that their function is not only consistent with the psychological interpretation of the early and late components, but also with the behaviour of these components in binocular rivalry. Finally, an attempt was made to integrate the findings that have implicated different structures in the generation of the late components. The next section attempts to determine the implications of this integrated scheme for a model of perception and attention, and more particularly for binocular rivalry.

4.3 A Theoretical Framework for Perception and Attention and a Context for Binocular Rivalry

4.3.1 The paradox of superior colliculus-association cortex function: some clues as to the physiological bases of perception and attention

In view of the proposed contribution of the superior colliculus-association cortex system to selective attention and conscious perceptual experience (cf. Chapter 3), this recent data, which implicates this same system in the generation of the late components of the evoked potential, appears to be paradoxical. In previous discussion it was argued that this system not only fails to yield a perceptual (phenomenal) adjunct to the information with which it is dealing, but is particularly concerned with information not currently at the focus of attention. We now see, however, that the electrocortical activity which this system generates is to be associated with conscious perceptual experience and with attention toward the stimulus which evokes such activity. This same paradox appears in relation to the rivalry data. It has been argued that the superior colliculus-association cortex system is responsible for the visual system's response to the non-dominant stimulus in rivalry, and yet we see that the evoked potential to such a stimulus fails to incorporate that component for which this system appears to be responsible.

The paradox only suggests itself however, because the evidence that relates the late component with the superior colliculus-association cortex system is misinterpreted. Thus, it must be remembered that though this system may

be responsible for the generation of the late components, it is the effects at visual cortex that are ~~monitored~~ productive of by the cortical evoked potential. With this appreciated, it may be suggested that <u>it is the interaction between the two visual systems that underlies the late components and the perceptual experience of the evoking stimulus</u>.

This hypothesis is consistent with the fact that neither system alone is able to mediate conscious perceptual experience. In the case of the superior colliculus-association cortex, this is most clearly revealed by the data relating to the residual visual capacity of patients suffering geniculo-striate lesions. And in the case of the geniculo-striate system, this is most clearly revealed by the observation that those components of the evoked potential that may be attributed to this system may be generated by a non-dominant stimulus in rivalry.

It may be concluded from all this, that the physiological correlate of the active process that is the presumed basis of perceptual experience is the interaction between the midbrain-posterior association cortex system and the geniculo-striate system, as revealed by the late component of the evoked potential. Since it has already been suggested, on the basis of the psychological correlates of the late components (particularly P300), that this active process is a matching process, whereby incoming sensory information is compared with the expectations based on an internal model of the world, we may postulate that it is with this psychological process that the interaction between the two visual systems correlates.

If we now look more closely at the function of such a matching process, within the context of a control system for adaptive behaviour, and more particularly at the supplementary processes that it must involve, it is possible

to be yet more specific about the complementary functions of the two visual systems in perception and attention.

4.3.2 Interpreting the interaction between the two visual systems.

MacKay (1956; 1969; 1972) considers perceptual experience in the context of a control system for adaptive behaviour, and argues persuasively that it reflects a matching, or hypothesis testing process, whose function is to match incoming sensory information against an internal model of the world. This model should not be construed as some form of pictorial reproduction of the outside world, but rather as a catalogue of "conditional expectancies" whereby every possible act is associated with a pattern of sensory information that should accompany its execution and result from its completion. The special act "do nothing" should also be considered to contribute to the catalogue.
Given that there is no mismatch, or disparity signal, two aspects of the system are confirmed. First, there is confirmation that the act executed was that which was intended. Second, and more importantly, the relevant conditional expectancy is reinforced, and it is in this sense that the matching process can be said to confirm a model of the world. If a significant mismatch does occur, however, then the nature of the disparity signal will serve both to modify the catalogue, and to initiate some act so that the incoming sensory information may again be tested against a conditional expectancy. This feedback process is envisaged to continue until the error signal is eliminated, in the same way that the difference in actual and desired

temperature is eliminated in a heating system that incorporates feedback control. The result of this is that the internal model, or catalogue, is made appropriate to the sensory information (cf. Fig. 19a).

When there occurs a change in receptor activity that may not be attributed to any act initiated by the system, there are two ways in which the process of adapting to the change (i.e. the selection of an appropriate model) may be made more efficient, and particularly quicker, than if the system relied solely on feedback control via the comparison process. Both of these possibilities involve the notion of feedforward control, whereby the error signals that result from such changes are anticipated.

Feedforward Control

The first type of feedforward anticipates change on the basis of past experience. Thus, whilst a change in receptor activity may not be attributable to some action, it may nevertheless be predictable as part of a sequence of changes that has regularly occurred in the past. This first type of feedforward makes use, therefore, of stored information regarding probable sequences of changes in the catalogue of conditional expectancies.

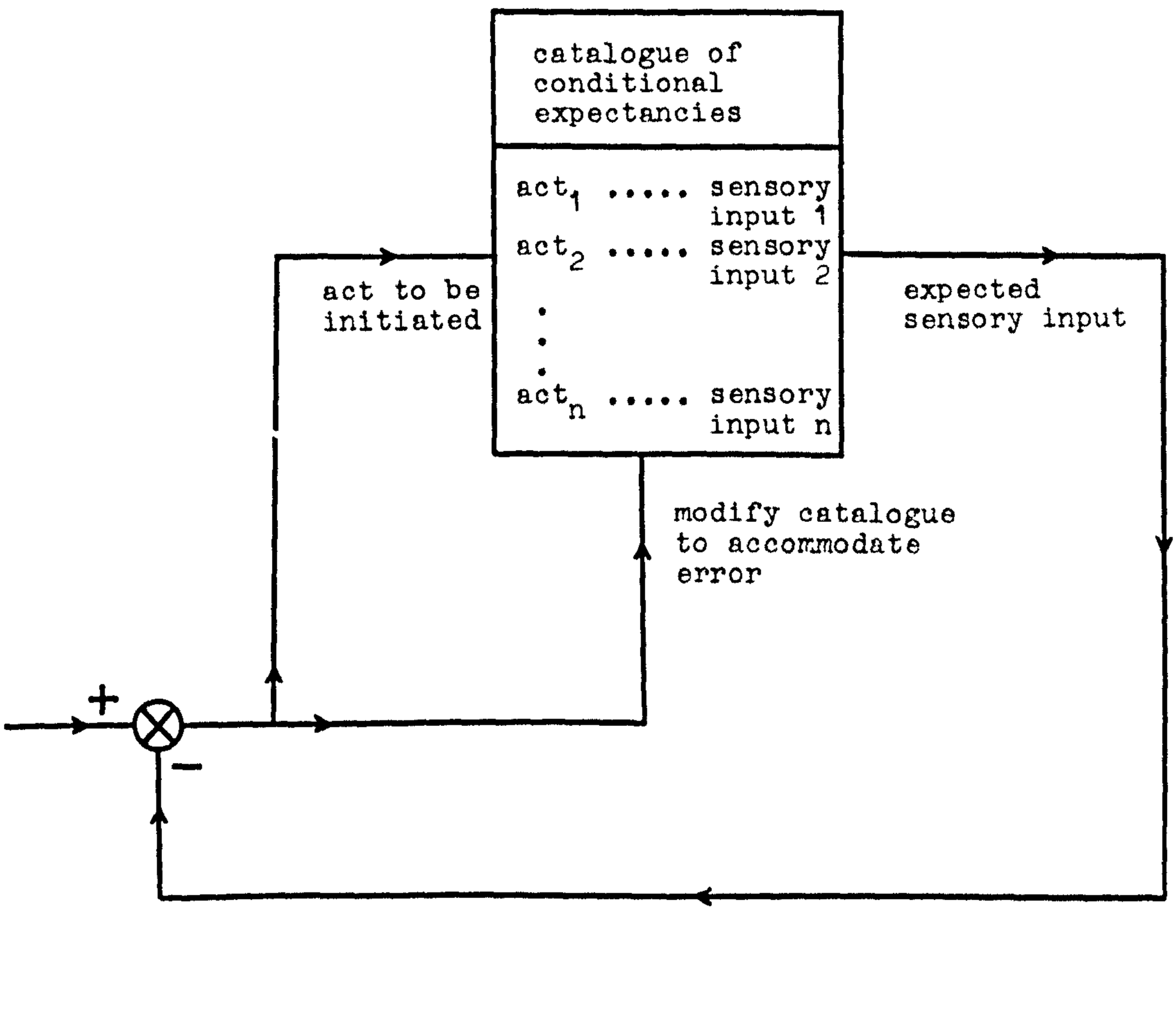
The second type of feedforward control is much more interesting, and in order to appreciate the principles upon which it may operate, it will be instructive to enquire why, when dealing with visual information, for example, relying solely upon feedback control would be inefficient and slow.

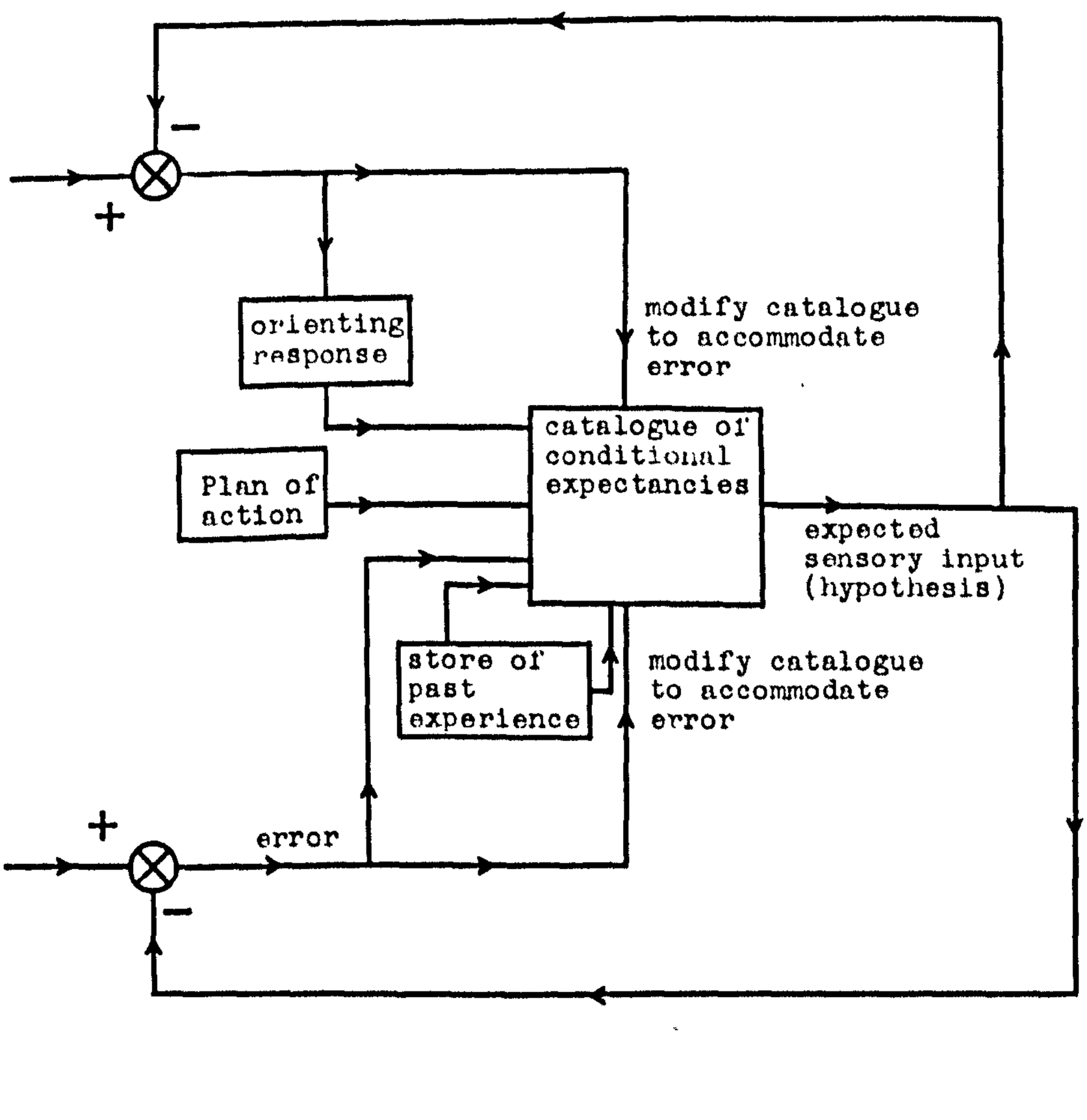
Since feedback control is suitable for the very fine

Figure 19 a,b

a. The matching process in the context of a control system for adaptive behaviour.

b. Additional factors contributing to the matching process, a distinction being made between feedforward and feedback control from the sensory data.


catalogue of conditional expectancies
act1 ..... sensory input 1
act2 ..... sensory input 2
actn ..... sensory input n
act to be initiated
expected sensory input
modify catalogue to accommodate error
+
−


−
+
orienting response
modify catalogue to accommodate error
catalogue of conditional expectancies
Plan of action
expected sensory input (hypothesis)
store of past experience
modify catalogue to accommodate error
+
error
−

adjustment of a system, we may expect that it will rely primarily on the most discriminating aspects of a receptor system. In specialising in this way, however, it may be less able to respond efficiently to the other, less discriminating regions of the receptor surface. More specifically, the advantages that come from feedback control may be best assured by its relying on information originating at the fovea, but this may be at the cost of being less able to monitor the activity of the less discriminating receptors that deal with information originating in the peripheral visual field. In addition, in view of the enormous range of feature filters that a highly discriminating system must possess, and upon which the comparison process may be based, the activity of only the restricted set of filters that is most relevant to the conditional expectancy to be matched, may be monitored (sampled) by the feedback controller. Consequently, feedback control may be slow to signal the occurrence of change if this were to involve features other than those relevant to the model currently being confirmed and refined.

There are at least two ways, therefore, in which feedforward may complement feedback control in adapting to an unexpected event: by monitoring the activity of a wide range of feature filters, particularly those features neglected by the feedback controller. We may say, then, that this feedforward system should be particularly concerned with information that is not currently at the focus of attention, whether this is because it originates at a different location from, or involves different features than, the information being monitored by the feedback control.

With respect to the first way in which feedforward may usefully complement feedback, there is an additional function for the feedforward mechanism which may best be appreciated by focusing on the systems handling of unexpected visual information. Thus, since an unexpected event is likely to occur in a location outside the domain of the feedback controller i.e. in the peripheral visual field, it would be useful if the feedforward mechanism were capable of initiating an act (orienting response) in order to present the relevant information to the feedback controller via the most sensitive regions of the receptor surface. To be capable of this additional function, the feedforward system must monitor the location of the unexpected information so that the act required to involve the feedback mechanism may be specified. However, this location information need only be approximate, since the fine guidance of the orienting act would best be under feedback control.

When we consider the second way in which feedforward may complement feedback, there is a yet additional function that it may usefully serve. Thus, the feedforward mechanism, in addition to signalling something of the location of the unexpected stimulus may also indicate something of its nature, and modify the catalogue accordingly. As a result of this modification, the sensory input to be expected would change, and feedback control would sample the activity of the relevant set of feature filters. According to MacKay[d], it is in this way, by narrowing the range of possibilities upon which feedback has to operate, that the feedforward of various key features of the sensory input may most usefully supplement evaluative feedback. Here, as with the orienting response function, we see that feedforward results in the sampling

of different aspects of the sensory input, though in this last instance there are none of the overt components of an orienting response. It would be consistent with present day usage of the term to refer to this shift in the stimulus features sampled by the feedback controller, as a shift in attention.

It is an additional requirement of a feedforward mechanism such as this, that it should be supplied with some information about what receptor activity to expect according to actions that are to be initiated, or according to past regularities. Thus, unless this mechanism was given information about the effects that, for example, an impending eye movement should have, it may interpret the effects when they occur as evidence for the real movement of a stimulus and on this basis initiate an eye movement, with disastrous results. Again, the prior information (a feedforward signal itself) as to what receptor activity to expect, need not be as detailed as that involved in evaluative feedback. We see then, that the feedforward mechanism should itself embody a comparison process whereby unexpected events may be identified as such. Thus, a distinction may be made between the initial matching process whose purpose is to signal the occurrence of a mismatch and initiate an orienting response and/or shift in attention, and the matching process that relies on the feedback receptor system in testing the new conditional expectancies selected by the feedforward signal. It is the latter that corresponds to the matching process that MacKay identifies with perceptual experience.

The control system of Figure 19a has now grown in complexity, and may be considered to involve the elements illustrated in Figure 19b. There are of course many aspects

of this scheme that are not justified on the basis of the discussion so far, and indeed to justify these aspects is beyond the scope of this thesis. The scheme does possess many interesting features that it is hoped will receive full discussion at a later date.

4.3.3 Two receptor systems?

To return to the problem of specifying the contribution of the two visual systems to the matching process, the most interesting question now is whether the feedforward and feedback control should make use of the same or distinct receptor systems. Though MacKay is not explicit on this point, he does imply that there should be a distinction in stating that "the system can cope with unpredictable disturbances either by simply allowing the sensory feedback to correct resulting errors, or (in addition) by using information from appropriate sense organs to feedforward approximate corrections to control signals, leaving less work for the feedback system" (MacKay, 1963, p.4, underscoring mine). We have already mentioned a number of reasons for believing that the receptor systems should be distinct in discussing the receptor characteristics that best suit the different types of control. Thus, whilst the feedforward system needs to be capable of monitoring information that originates in locations beyond the domain of the feedback system, it need not have the same discriminatory powers as the latter with respect to spatial parameters, since its primary function is to signal approximate corrections to the catalogue of conditional expectancies. As MacKay indicates, the filters required for the feedforward signals can be very crude and yet still yield an enormous improvement in speed of adaptation. Interestingly, in the case of vision, this last characteristic may almost be regarded as a requirment of the first. Thus, since a novel stimulus that appears in the visual field is likely to do so via the periphery, and at a depth for which the ocular system is not accommodated, its image may be rather poor in quality. Furthermore, with its concern for signalling the appearance of unexpected information, the feedforward system, in contrast to the feedback system, should be particularly sensitive to those stimulus features that

in general indicate that a stimulus is novel. Thus, it should be especially sensitive to the movement of a stimulus and to changes in stimulus parameters in general.

Finally, one added requirment of the feedforward system is that it performs its function relatively quickly, so that all those processes involved in accommodating the catalogue, however approximately, to the new information may be completed whilst the raw data is still available for evaluative feedback, and before there is further change. With this refinement, the feedforward mechanism would, in a very real sense, anticipate the occurrence of an error signal in the feedback system.

The reader will already have appreciated that these characteristics of the feedback and feedforward receptor systems correspond to those discovered for the geniculo-striate and superior colliculus-posterior association cortex systems respectively. In the geniculo-striate system we do observe the high sensitivity to spatial information and the enormous bank of highly specific feature filters that are essential for a feedback receptor system. More intriguing however, are the properties of the superior colliculus-posterior association cortex system that identify it as a feedforward receptor system. Considering, in order, the properties to be associated with such a control system, we first appreciate that this neurophysio-logical system is equally concerned with sensory information originating in theperipheral and central visual field (Trevarthen, 1968; Ikeda and Wright, 1972). Second, although cells in this system, particularly in the posterior association cortex, have quite elaborate preferred stimuli (Gross, 1973) they are, compared to cells comprising

the geniculo-striate complex, relatively insensitive to such spatial parameters as stimulus orientation, size and location (Gross, 1973; Wickelgren-Gordon, 1972; Dow and Dubner, 1969). Moreover, with regard to the possible necessity of such relaxed sensitivity, Ikeda and Wright (1972; 1974) have spotlighted the significance of the fact that transient neurones, unlike sustained neurones, are able to respond to defocus_ed retinal images. This, they argue, is critical for any neural system that is to be responsible for initiating a response to an image that originates in the peripheral visual field, and from a distance other than that to which the eyes are accommodated. Third, those stimulus features to which the superior colliculus-association cortex system is particularly sensitive, are well suited to this systems hypothesized role in selectively responding to change or unexpected events (cf. Ikeda and Wright, 1972 especially, but also Schiller and Koerner, 1971; Dow and Dubner, 1969). Moreover, since one would expect this sensitivity to change to be mirrored in an insensitivity to unchanging input, it is understandable that the superior colliculus-posterior cortex system, in sharp contrast to the geniculo-striate system, readily habituates (Horn and Hill, 1966; McIlwain and Buser, 1968; Dow and Dubner, 1969; Wright, 1969; Schiller and Koerner, 1971). Finally, with respect to the speed with which the feedforward system fulfils its function, it is interesting to note that Ikeda and Wright (1972) have demonstrated that the transient neurones that comprise the retino-superior colliculus pathway display relatively fast conduction velocities compared to the most important category of neurone (sustained) in the geniculo-striate complex.

It is clear that these features of the second visual system recommend its nomination as a feedforward system that is primarily responsible for signalling the appearance

of unexpected and unattended stimuli. Indeed, in view of the hypothesized involvement of a feedforward system in the initiation of an orienting response and/or shift of attention, there are still further facts to recommend this function for the superior colliculus-posterior association cortex system. Evidence has already been discussed (Chapter 3) which demonstrates that the functional integrity of this system is necessary for orienting behaviour, for the monitoring of unattended information, and for redirecting attention. A final, closer look at the eye movement component of the orienting response further confirms this theory.

Though the superior colliculus has traditionally been assigned an intermediary role in eye movements, being thought to provide the detailed target information for their accurate guidance, recent evidence not only suggests that it is instrumental in <u>initiating</u> a shift in in fixation, but confirms the more general role that is assigned to it in the present discussion. Wurtz and Goldberg (1972a) have commented that the coarse nature of the receptive field properties of cells in superior colliculus is not suited to this traditional function, since only relatively approximate information as to target location may be yielded. In fact, these authors provide experimental evidence that there is not a rigid association between the neuronal activity in superior colliculus, and the occurrence of an eye movement. On the basis of their results they suggest that the superior colliculus is concerned with signalling the appearance of objects that are <u>not</u> currently at the focus of attention, initiating a shift in attention, and supplementing this with an orienting eye movement if necessary. Wurtz and Gddberg, then, in their suggestions are encouraging a feedforward interpretation of the superior colliculus-association cortex system (cf. in particular, Wurtz and Goldberg, 1972d, pp. 593-594). Of particular interest in this respect

is their finding that ablation of the superior colliculus does not reduce the accuracy of an eye movement, but rather, simply increases its latency. This is consistent with the feedforward model, since the fine adjustment of eye movements would be mediated by a feedback mechanism with its very sensitive receptor system, and since it is primarily to speed the process of adapting to change that is the function of a feedforward system.

To return to the problem of specifying the nature of the contribution of the two visual systems to the matching process that was earlier presumed to be reflected in their mutual interaction, we see that the geniculo-striate and superior colliculus-posterior association cortex systems may be assigned complementary functions in an outline model of perception and attention. The latter system is thought to feed forward information concerning unattended information and unexpected information, to modify the catalogue of conditional expectancies, and finally to initiate an act (orienting response or shift in attention) that will serve to bring these modifications under feedback control for confirmation and refinement. The geniculo-striate system is thought to provide this feedback controller with its raw data. The superior colliculus-association cortex is capable of initiating the feedback matching process and, according to the revised conditional expectancies, of guiding its sampling of the sensory information provided by the geniculo-striate cortex system. We see then, that assigning such complementary functions to the two visual systems confirms the earlier conclusion that their interaction involves a matching process whereby sensory information is compared with the expectations of a currently held model of the world.

To the extent that the late components in the evoked

potential reflect the interaction between the two systems and also correlate with perceptual experience, the evidence discussed in previous sections confirms MacKay's belief that perception reflects a matching process. However, in the previous discussion of whether P300 reflected this same matching process, the problem of specifying just what aspect of this process was important was considered, and it was suggested then that it was not the signalling of a mismatch, but rather the successful matching of a model. The present scheme supports this interpretation of the evidence, and even goes so far as to separate the initial matching process that is responsible for signalling the occurrence of a mismatch in the first instance, from the feedback matching process that serves to confirm and refine the modified catalogue suggested by the nature of this mismatch signal. That it is the latter that correlates with perceptual experience (or more specifically P300) is further supported by the results of a recent study (to be more fully discussed below) that has shown that under conditions where the successful matching of a model should be delayed, but not the original mismatch, so the appearance of the late component (P300) of the evoked potential is delayed.

Finally, the scheme accommodates the close relationship, synonymity almost, between perception and attention, in that what is currently being perceived and what is currently being attended to are both specified by the conditional expectancy under test.

4.4 Summary and Implications for Binocular Rivalry

In this chapter, it was first argued that a meaningful distinction could be made between the early and late components of the cortical evoked potential. The interpretation of these different components, in terms of the psychological processes they reflect, was shown to be consistent with the evoked potential correlates of binocular rivalry, when this phenomenon was considered in the context of an "active" model of perception. Thus, whilst a number of studies were reviewed which demonstrated that the conditions leading to the generation of the early components are not sufficient for conscious perception, neither the latency nor the amplitude of these components could distinguish between a dominant (perceived) and non-dominant (unperceived) stimulus in binocular rivalry. Since the early components had previously been associated with the cortical discrimination of a stimulus, these data encouraged the more "active" model of rivalry, which considered conscious perception to reflect processes undertaken subsequent to the discrimination and recognition of a stimulus. In line with such a model, the later components of the evoked potential were shown to distinguish the dominant and non-dominant stimuli in rivalry, being detected only in the former case. Moreover, other data were discussed which indicated that these later components are to be associated with conscious experience, "endogenous processes", and in particular with some internal aspect of the orienting response, such as the neural matching of sensory input with an internal model of the world.

When consideration was next given to the physiological structures that appear to contribute to the generation of the early and late components of the evoked potential, some proposals were made regarding the physiological

processes which most directly correlate with perceptual experience. Relying heavily on the previous discussion of the distinction between two visual systems, and on recent findings concerning the contribution of the midbrain-posterior association cortex system to the generation of the evoked potential, it was proposed that the interaction between the two visual systems, and more specifically between the posterior association cortex and primary visual cortex, was a physiological process which directly correlated with conscious perceptual experience. Though cortical activation by the ascending reticular system has previously been linked with conscious perceptual experience, particularly in discussions of subliminal perception, it was contended that the evidence for this is less direct than that which implicates the interaction between the two visual systems. Indeed, it was pointed out that since recent data demonstrate that the RAS has its (reciprocal) cortical connections with association cortex, rather than primary cortex, the contribution of the RAS to activity in primary cortex and to perceptual experience, is likely to be made via this interactive process between primary and non-primary cortex.

Bearing in mind the link between this interaction of the two visual systems and perceptual experience, that is best illuminated by the late components of the evoked potential, a more specific interpretation was suggested for this interaction and for the separate function of each of the two visual systems. Drawing on a control systems approach to perception in the context of adaptive behaviour, an outline model of perception and attention was presented. In this, perceptual experience was considered to reflect a sampling and matching process that provides feedback as a check that incoming sensory data conform to expectations based on a catalogue of conditional expectancies (model of the world). The conditional expectancy under test was

thus considered to determine the content of perceptual experience. It was further suggested that the matching process should be served not only by a highly discriminating receptor system responsible for mediating feedback, but also by a receptor system responsible for generating feedforward signals to the catalogue of conditional expectancies. A variety of facts indicated that there should be two receptor systems, and those receptor characteristics that, it was thought, would best serve feedforward control were just those characteristics that could be identified with the superior colliculus-posterior association cortex system. In the outline model therefore, this latter system was assigned the role of a feedforward mechanism, whose function was to monitor information not currently at the focus of attention, and to anticipate a feedback error signal by feeding forward approximate corrections to the catalogue of conditional expectancies. In addition, it was argued that it should be a supplementary function of a feedforward system to initiate an orienting response and/or shift in attention necessary to ensure that the feedback system sampled the relevant sensory information. Assigning this supplementary role to the midbrain-posterior association cortex system is consistent with the available data. In this respect, of particular interest was the finding that ablation of the superior colliculus gives rise not to less accurate orienting eye movements, but to an increase in their latency. Thus, whilst the accurate guidance of eye movements is best mediated by feedback control, it is to <u>speed</u> the process of adapting to change that is the important function of a feedforward system. Indeed, though the effects of inferotemporal cortex lesions are more complex than those resulting from superior colliculus ablation, it is interesting that Gross (1973) suggests that the fundamental effect is to retard the learning process.

In serving the function assigned to it, the feedforward system was thought to incorporate processes that would allow expected and unexpected sensory information to be distinguished. Thus, the feedforward system was considered to itself incorporate a matching process that would signal a relatively gross mismatch between the actual and expected information. This matching process was thought to be the one considered by others as the essential and preliminary component of the orienting response. The outline model therefore separates the initial matching process, that is responsible for signalling the appearance of a mismatch in the first instance, from the feedback matching process that serves to confirm and refine the modified model of the world suggested by the nature of this mismatch signal. It is argued that it is the latter matching process that correlates with perceptual experience.

Whilst a feedforward role is assigned to the superior colliculus-association cortex complex, the geniculo-striate system is identified as the feedback receptor system. In this scheme, then, the interaction between non-primary and primary cortex is considered to reflect the sampling and matching of the sensory data provided by the geniculo-striate system in order to confirm and refine the conditional expectancies (model of the world) under test.

4.4.1 Implications for the explanation of rivalry

Though the scheme for perception and attention outlined above has made full use of the data relating to binocular rivalry, it goes beyond that which these data alone could justify. We may now, therefore, reconsider the phenomenon and look at the implications of this scheme for its explanation.

4.4.2 The mutually exclusive nature of rivalry

In Chapter 2, it was pointed out that the mutually exclusive nature of rivalry has encouraged the belief that there exists a reciprocal inhibition between the two monocular systems, and that it is this that is responsible for the perceptual suppression. Since the available data do not attribute any significance to this possibility, we may ask if there is anything about the scheme that may accommodate this feature of rivalry.

Implied in the preceding sections has been the notion that rivalry reflects fundamental perceptual processes and the evidence discussed so far is consistent with this. If this notion is correct, not only should the theory outlined above be able to accommodate the mutually exclusive nature of rivalry, but the same phenomenon should be observed in other contexts.

MacKay (1969) has used the mutually exclusive nature of perception in the case of ambiguous figures to support his thesis that perceptual experience reflects a matching, or hypothesis testing process. From all the mechanisms

that it has been proposed reflect perceptual experience (for example, microelectrode recording of the activity of single cells has recently encouraged the notion that it is the activity of a "filtering and classifying" system that is reflected in perceptual experience) MacKay states that such a process is the only one that would not allow the simultaneous perception of both. His argument is, presumably, that only one interpretation may be tested at any point in time because the internal model of the world can allow for only one object to occupy a particular location. That this also is the essence of the exclusive nature of binocular rivalry, is suggested by the fact that when presented with potentially rivalrous sensory information, subjects may occasionally perceive, as an alternative to rivalry, one of the images to lie in front of the other (Helmholtz, 1911; Alexander, 1951; Bagby, 1956). The "non-dominant" image in such cases is reported to appear "through" the dominant one. Distorting the sensory information in this way, therefore, avoids the incompatibility that arises when different objects appear to be occupying the same location (cf. Kolers, 1972). In this light it is intriguing that when the monocular images represent objects that are not incompatible, in that they may indeed originate from the same spatial location, then rivalry is much less likely, and fusion much more likely. The presentation of a parrot to one eye, and a cage to the corresponding area of the other eye, is a case in point.

Other researchers also have suggested that a pre-requisite for rivalry is the simultaneous presentation of information that indicates the existence of different objects in the same spatial location. Thus, Harris and Gregory (1973) state that rivalry between illusory contours is explicable "if rivalry is a function of incompatible object information from the two eyes, rather than merely retinal disparity exceeding Panum's limit" (p.246).

4.4.3 The "suppression" in rivalry.

That the non-dominant stimulus favours the selection of a model-to-be-matched that is incompatible with that based on the dominant stimulus, is one reason why the non-dominant stimulus fails to contribute to perceptual experience; it can not be incorporated, however approximately, in the model currently being tested by the feedback matching process.

There is a second sense, however, in which the scheme predicts that the non-dominant stimulus must necessarily fail to contribute to perceptual experience, and this also relates to the problem of why it is that a model-to-be-matched that does not incorporate all the sensory information is not immediately disconfirmed by the feedback matching process. Implied in the above scheme is the notion that the feedback matching process is necessarily selective in its sampling of the sensory information. It may be suggested, therefore, that a non-dominant stimulus fails to contribute to perceptual experience because the corresponding sensory information in the feedback receptor system is not sampled. In this way, information regarding the non-dominant stimulus, that is not incorporated in the model under test, fails to contribute a feedback error signal. This aspect of the scheme, which will be elaborated and defended in later sections, is able to accommodate the partial suppression of rivalling images and some of the between-subject variation in the rate of binocular rivalry alternations.

Subliminal Perception

It will be appropriate at this point to consider the general implications of this scheme for subliminal perception. Thus, for the same two reasons that a stimulus

may be non-dominant in rivalry, so in other contexts, it may be discriminated and yet remain "subliminal". However, the scheme also allows for subliminal perception in yet other ways. If we consider the case of stimuli that are very weak, of low illumination or low contrast, then we may imagine that whilst the feedforward system is able to recognize the stimulus, signal approximate corrections to the catalogue of conditional expectancies and initiate some component of the orienting response, the stimulus is unable to significantly change the feedback receptor system to enable these corrections to be confirmed. Evidence has already been discussed (Chapter 3) which suggests that the superior colliculus-association cortex system is more able than the geniculo-striate system to respond to stimuli under low illumination and low contrast conditions. Moreover, experiments 1 and 3 both demonstrated that the system responsible for mediating the response to the non-dominant stimulus (identified as the superior colliculus-association cortex) is also capable of dealing with stimuli that fall below the awareness threshold. Finally, an additional implication of the scheme is that any behavioural effects resulting from subliminal stimuli are more likely to result from the superior colliculus-posterior association cortex system's response to this stimulus, than from the geniculo-striate system.

4.4.4 The alternations in perceptual dominance

It has been proposed that a prerequisite for rivalry is the simultaneous presentation of two stimuli that demand the selection of incompatible models of the world, in the sense that different objects would have to occupy the same location in space. Because of this incompatibility, it follows that at any time only one of the stimuli is incorporated in

the model being matched, and it is further assumed that only the sensory information pertaining to this is sampled by the feedback matching process. Since a further prerequisite for rivalry alternations appears to be that the stimuli are unchanging, the system would be expected to accurately match the relevant sensory information, and in accordance with Sokolov's (1963) understanding of habituation, the system should habituate to the currently dominant stimulus that is being successfully matched. However, since the currently non-dominant stimulus is not incorporated in the model being matched, the system would be expected to recover from its habituation towards this stimulus, that occurred during its preceding dominance phase, until eventually it would be regarded as sufficiently "unexpected" to warrant the selection of a new model-to-be-matched, resulting in an alternation in dominance.

Recommending this explanation of the alternations is the fact that it ties together the different aspects of the evidence concerning the alternations; evidence which indicates that it is the recovery from habituation to the non-dominant stimulus that takes precedence over the habituation to the dominant stimulus. Thus, in the scheme, responsibility for initiating an orienting reaction to a stimulus that does not conform to the currently dominant model, is assigned to the feedforward system, viz. the superior colliculus-posterior association cortex system. Consistent with this, the discussion in previous sections of this thesis has implicated this neural system in the observed sensitivity of the visual system to the non-dominant stimulus in rivalry. Moreover, the fact that this system seems to be concerned primarily with unattended (non-dominant) information, is consistent with the literal interpretation of Levelt's thesis, for which support has been obtained throughout.

4.4.5 Evoked potential correlates of rivalry

This theoretical scheme not only accommodates the results of the evoked potential study (Experiments 4 and 6) but suggests how the discrepancy with the results from the reviewed studies may be resolved. It will be remembered that whilst a number of studies indicated that a non-dominant stimulus in rivalry should not contribute any late components to the evoked potential, in Experiments 4 and 6 such late components were observed, albeit with increased latency and reduced amplitude. In the discussion of these two experiments, it was suggested that the presence of the late components was attributable to the relatively immediate perceptual effects of the stimulus responsible for the evoked potential. Since the scheme assumes that the shift in dominance is in essence an orienting response, then it would predict the presence of late components in the evoked potential. It will be noted that in attempting to avoid contaminating the evoked potential with response effects, the nature of the stimulus that was chosen helped ensure the initiation of an orienting response. The unpredictable onset of the stimulus was one such feature. Returning to the discrepancy with other studies, then, it may simply be noted that the experiments which failed to reveal a late component to the non-dominant stimulus, also avoided the elicitation of an orienting response (immediate shift in dominance) by, for example, employing a repetitive and predictable non-dominant stimulus to evoke the cortical potential.

At the risk of going far beyond that which the existing data could justify, the scheme offers a tentative explanation of the increased latency of the late components in the non-dominant condition. Thus, according to this scheme, the pattern-reversal of the vertical grating in this

condition would generate a mismatch signal and thereby lead to the selection of a new model-to-be-matched. We may assume that the selection of this model, and its subsequent test via feedback, should require less time when the currently dominant stimulus is the vertical grating itself and not the horizontal grating. In the former case the new model is very similar to the previously dominant one, and the same stimulus features are relevant to the feedback mechanism.

If as the scheme implies, the late components reflect the successful matching of a model, then we may predict their increased latency from the fact that this extra processing is involved when the pattern reversal occurs whilst the vertical grating is non-dominant. Some recently published results add some support to this rather speculative interpretation. Posner et al (1973) recorded the evoked potential to the second of two letters that were presented visually and sequentially. The evoked potential was averaged separately for those instances where this second letter "matched" the first (had the same name), and those instances where it was different. Distinguishing the potential in these two situations was a late positive component, with a latency in the 300-400 msec. range. When the second letter did not match the first, the latency of this component was increased and its amplitude reduced. With the earlier components being the same in the two conditions, these results mirror the effects observed in the binocular rivalry experiment. For Posner et al. this result indicated "that the evoked potential differences ....arise because when a stimulus matches a previous input it starts to occupy the limited-capacity (conscious) mechanism at an earlier point" (p.10). They suggest then, that the presence of a stimulus that deviates from what the subject expects on the basis of a model, delays the late positive

component because of "prolonged or enhanced processing of a mismatch" (p.2). Furthermore, in an additional experiment, Posner et al (1973) were able to identify this component as P300 by showing that it was enhanced when subjects had to count either the number of mismatches or the number of matches. In view of all this, it is particularly interesting that in another paper (Posner and Boies, 1971) Posner states that "The finding that presentation of the first letter improves the efficiency of handling an identical second letter suggests that the first letter changes subject's sensitivity to a letter of identical form. One way of conceptualizing this is in terms of Sokolov's neural model idea. The first letter serves as a model of what the subject is looking for, when the second letter matches it, processing proceeds rapidly; if it does not, further tests are made" (pp.399-400).

We see then, in this work, some justification for entertaining the rather speculative explanation of the effects on the late components that were observed in Experiments 4 and 6. Moreover, it confirms the earlier interpretation of the data relating to P300 which suggested that this component, and conscious perceptual experience, do not reflect the occurrence of a mismatch, but rather the successful matching of an internal model.

4.4.6 Returning to the "negative evidence"

At this point it may be appropriate to return to the "negative evidence" that was reviewed in Chapter 2. It will be remembered that Fox and his colleagues discovered that subjects took longer to respond to a stimulus when this was introduced in to the non-dominant field, than when it was introduced in to the dominant field. They

interpreted this as indicative of a reduction in sensitivity, and hence favoured the theory that rivalry involves a suppression mechanism. It was suggested in the previous mention of these results however, that an alternative to the suppression interpretation could be based on the assumption that it takes some time to "shift attention" to the opposite monocular channel, and that it is this that is reflected in the reaction time. The theoretical scheme outlined above offers more specific interpretation of this alternative explanation, suggesting that the increased latency may result from the fact that the matching process has to be redirected so that the activity of feature analyzers that are driven by the opposite eye may be monitored or sampled.

4.4.7 The problem of prediction

The major criticism of the "active" or cognitive approach to perception, as exemplified by the work of MacKay (1969) and Gregory (1966), relates to the difficulty with which testable predictions may be generated, and this is ascribed partly to the vague and mentalistic concepts that such approaches involve. With regard to this last point, it must be appreciated that, though such notions as "sampling information" and "confirming expectations" may hint at the existence of an homonculus, they need not be interpreted in this way. This is best illustrated by the fact that MacKay is able to incorporate such notions in artifical control systems. Returning to the first point however, this is not so easily dealt with, and indeed, the author knows of no experiment that was undertaken in order to test a prediction from an active model such as MacKay's.

It is with the problem of deriving and testing predictions from the above skeleton model of perception and attention, as it applies to rivalry, that the third part of this thesis is concerned. Though at this stage the

predictions are admittedly rather general and qualitative, they do, nevertheless, allow the model to be evaluated and refined. In this respect, it will be seen that anchoring the components of the model to physiological mechanisms proves most fruitful. The first problem that is dealt with in the next section, however, is not one relating directly to physiological mechanisms.

PART 3

PREDICTIONS BASED ON THE THEORETICAL FRAMEWORK

CHAPTER 5 STOCHASTIC PROPERTIES OF BINOCULAR RIVALRY ALTERNATIONS

In view of the fact that the processes underlying rivalry are considered to be rather fundamental perceptual processes, that are not at all specific to situations that involve the separate presentation of different stimuli to the two eyes, the most obvious prediction from the model presented in the previous chapter, is that the same processes should reveal themselves in a variety of perceptual phenomena. In other words, the characteristics of binocular rivalry should be observed in other contexts.

It was suggested in the previous chapter, that the same underlying processes were being reflected in the mutually exclusive nature of binocular rivalry and ambiguous figures. There is an additional feature, however, that is common to both phenomena, namely the alternation process, and there is here evidence that similar processes are involved in the two situations. For example, a two-parameter gamma distribution has been found to describe the frequency distribution of the dominance phase durations of either alternative percept, in the case of ambiguous figures such as the Necker C ube and Schroeder staircase (De Marco, Allazetta, Rinesi, and Bartolini, 1972), and in binocular rivalry (Fox and Herrmann, 1967). Moreover, in both cases, additional analyses reveal that successive dominance phase durations are independent.

Since only Fox and his colleagues have studied this independence aspect of rivalry, and then only with a single pair of achromatic stimuli, it was considered worthwhile to determine (i) whether successive dominance phase durations are independent for other achromatic stimuli

and also for chromatic stimuli, and (ii) if a two-parameter gamma function is able to describe the frequency distribution of dominance phase durations in these two cases. Furthermore, the opportunity was taken to further refine the analysis of Fox and Herrmann (1967) by, for example, employing a non-parametric test of independence based on Kendall's (1973) treatment of time series.

In three different, though related ways, previous experiments have indicated that successive rivalry phase durations are independent: (1) Altering the stimulus parameters of just one rivalling field has been demonstrated to have asymmetrical effects on the course of rivalry. Thus, Fox and Rasche (1969) and Levelt (1966) have reported that increasing the stimulus strength (e.g. contrast) of a rivalling image causes a change in the mean duration of dominance of the contralateral image only: the mean duration of dominance of the changed stimulus remains unaffected. (2) Direct statistical tests of sequential dependency have yielded negative results. Blake, Fox and McIntyre (1971) and Fox and Herrmann (1967) undertook an autocorrelation analysis on the successive phase durations, in addition to determining the average absolute slope of successive durations (a test of first-order dependencies) in a manner outlined by Lathrop (1966). Both procedures failed to provide support for the dependence hypothesis. (3) The fact that a two-parameter gamma distribution has been found to describe the frequency distribution of the rivalry phase durations reasonably well (Blake et al, 1971; Fox and Herrmann, 1967; Levelt, 1967) is consistent with the sequential independence of successive phases (cf. Fox and Herrmann, 1967).

Data from the "blank" condition of Experiment 1, and from an additional study, provided an opportunity to test

again the notion that the durations of successive rivalry phases are dependent. It will be remembered that Experiment 1 employed rivalling red and green homogeneous fields, and so the results permitted the previous findings (based entirely on rivalry between achromatic stimuli) to be extended to the colour domain.

Chromatic stimuli

The blank condition of Experiment 1 provided data from two, separate 90-sec. trials for each subject. Although 44 subjects contributed to the total set of data, results from only 33 of these were incorporated in the present analysis, the sole requirement for inclusion being that for each trial the number of alternations was sufficient to permit the type of analysis planned.

Achromatic stimuli

In this experiment, subjects reported on the rivalry alternations between competing vertical and horizontally oriented square-wave gratings that were used in the evoked potential study, and which were presented to the left and right eyes, respectively (cf. Fig. 13).

Subjects were provided with a single push button for use with their right hands, and were instructed to press this whenever and for as long as the smaller (vertical) grating was suppressed. On the one 90-sec. trial that each subject completed, the responses were recorded on one channel of an Esterline Angus pen recorder, in the manner of Experiment 1.

Eighteen undergraduate students attending University College served as subjects.

	Replicate	
Correlation coefficient		
Chromatic stimuli		
Red	.802	.840
Green	.925	.834
Achromatic stimuli		
Horizontal	.771	
Vertical	.716	
Regression coefficient		
Chromatic stimuli		
Red	.629	.621
Green	.813	.785
Achromatic stimuli		
Horizontal	.751	
Vertical	.476	

Mean values for the correlation and regression coefficients reflecting the positive linear relation between the standard deviation and mean of the dominance phase durations.

Table 26

		Replicate
Regression coefficient		
Chromatic stimuli		
Red	.1440	.0901
Green	.0857	.0435
Achromatic stimuli		
Horizontal	-.0268	
Vertical	.0901	
Associated F values		
Chromatic stimuli		
Red	.3946	.2181
Green	.1722	.1812
Achromatic stimuli		
Horizontal	.2204	
Vertical	.1518	

Mean values for the regression coefficients and associated F values reflecting the absence of any temporal trends in the sequence of phase durations.

Table 27

		Replicate
Lathrop statistic		
Chromatic stimuli		
Red	.9745	1.012
Green	.9958	.988
Red/Green	.9775	1.0212
Achromatic stimuli		
Horizontal	1.039	
Vertical	1.059	
Horizontal/Vertical	1.002	
Associated z values		
Chromatic stimuli		
Red	-.200	.080
Green	-.030	-.120
Red/Green	-.1615	.169
Achromatic stimuli		
Horizontal	.280	
Vertical	.420	
Horizontal/Vertical	.244	

Mean values for the lathrop statistic and associated z scores reflecting a sequential independence within the sequences of dominance phase durations.

Table 28

z values		Replicate
Chromatic stimuli		
Red	.00	.02
Green	.12	-.04
Red/Green	.20	.25
Achromatic stimuli		
Horizontal	.13	
Vertical	.48	
Horizontal/Vertical	-.43	

Mean values for the z scores associated with the number of turning points analysis.

Table 29

	Phase Length	Frequency Obs'd	Exp'd	Chi-Squared
	Chromatic Stimuli			
Red	1	5.15	4.89	
	2	1.87	1.97	1.08
	3	.51	.63	
Green	1	4.66	4.78	
	2	2.33	1.92	4.79
	3	.39	.61	
Red/Green	1	12.03	11.45	
	2	4.63	4.85	1.26
	3	1.78	1.68	
	Replicate			
Red	1	5.15	5.05	
	2	2.00	2.03	.07
	3	.63	.65	
Green	1	4.96	4.95	
	2	1.96	1.99	.19
	3	.57	.63	
Red/Green	1	13.00	11.83	
	2	4.57	5.02	4.69
	3	1.66	1.80	
	Achromatic stimuli			
Horizontal	1	4.38	4.07	
	2	1.50	1.60	.48
	3	.50	.50	
Vertical	1	5.11	4.14	
	2	1.61	1.63	5.12
	3	.27	.51	
Horizontal/ Vertical	1	8.38	9.76	
	2	4.33	4.11	4.22
	3	1.72	1.41	

Note: Also tabled are the corresponding chi-squared values, the value required for significance being 5.99.

The mean observed frequencies for the different phase lengths together with the mean expected frequencies.

Table 30

	Lag				
	1	2	3	4	5
	Chromatic stimuli				
RG	.166	.068	.092	-.029	-.002
GR	.172	.119	.050	-.050	-0.03
RR	.103	.104	-.006	.044	-.079
GG	.043	.017	-.049	-.070	-.054
	Replicate				
RG	-.025	-.030	.042	.032	.023
GR	.055	.083	.026	-.014	-.043
RR	.027	.064	-.046	.006	-.051
GG	.030	-.064	-.012	.036	-.085
	Achromatic stimuli				
HV	-.012	.066	-.009	-.155	.049
VH	.206	-.005	.016	-.061	-.101
HH	-.023	.005	-.105	-.005	0.03
VV	-.077	.011	-.039	-.122	.084

Note. H = horizontal grating and V = vertical grating.

Mean values for the autocorrelation coefficients, through lags 1-5, between RG-successive red and preceding green phases, GR-successive green and preceding red phases,etc.

Table 31

Figure 20

The mean autocorrelation coefficients that are presented in Table 31 are here illustrated in the form of correlograms. The vertical bars delimit the range of values spanned, for both positive and negative coefficients, by the mean of the standard deviations associated with each of the obtained values. a and b = chromatic stimuli, b = replicate data, c = achromatic stimuli.

○ = RG for a and b, and = HV for c;

● = GR for a and b, and = VH for c;

△ = RR for a and b, and = HH for c;

▲ = GG for a and b, and = VV for c.

cf. Table 31 for symbol code.

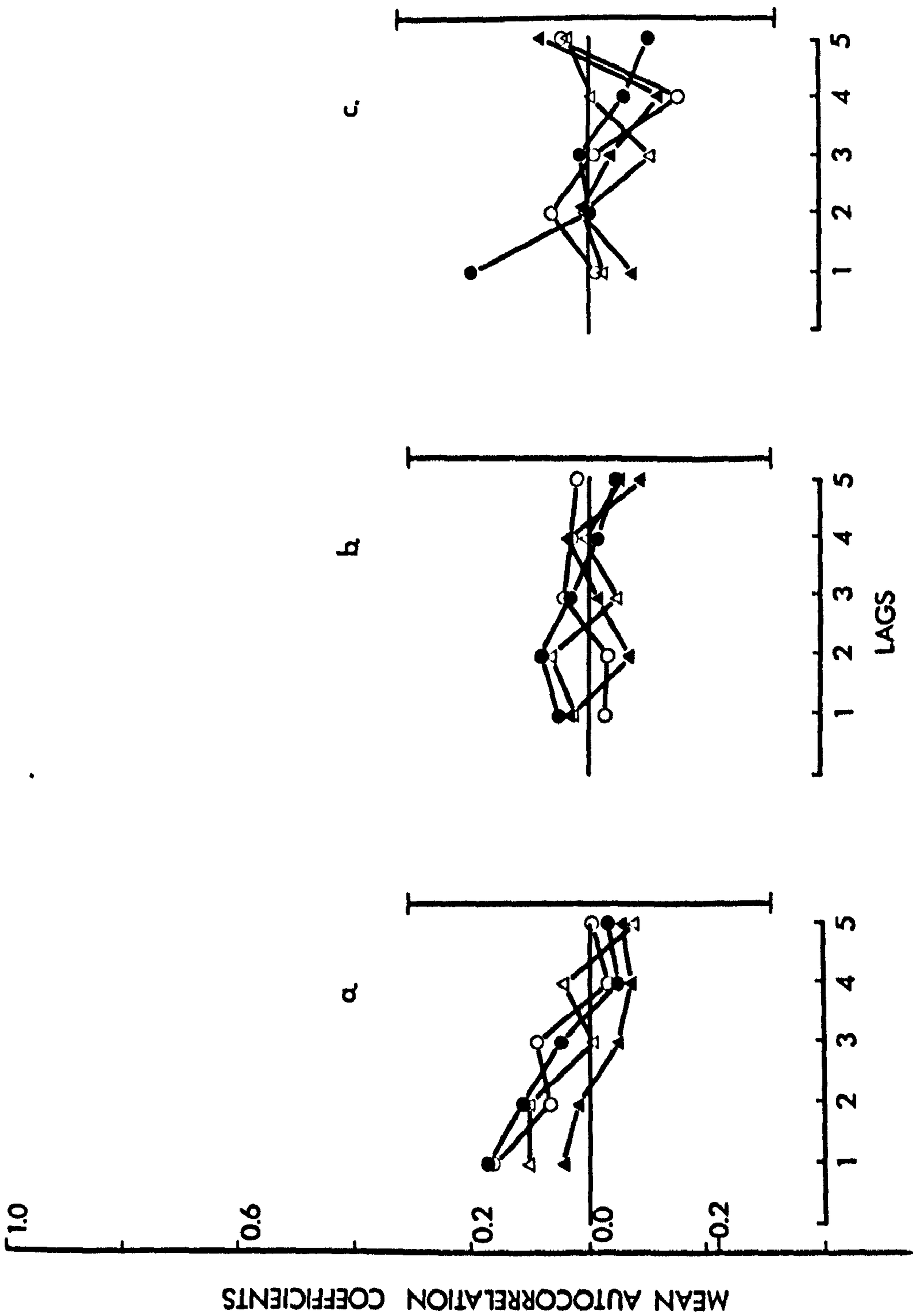
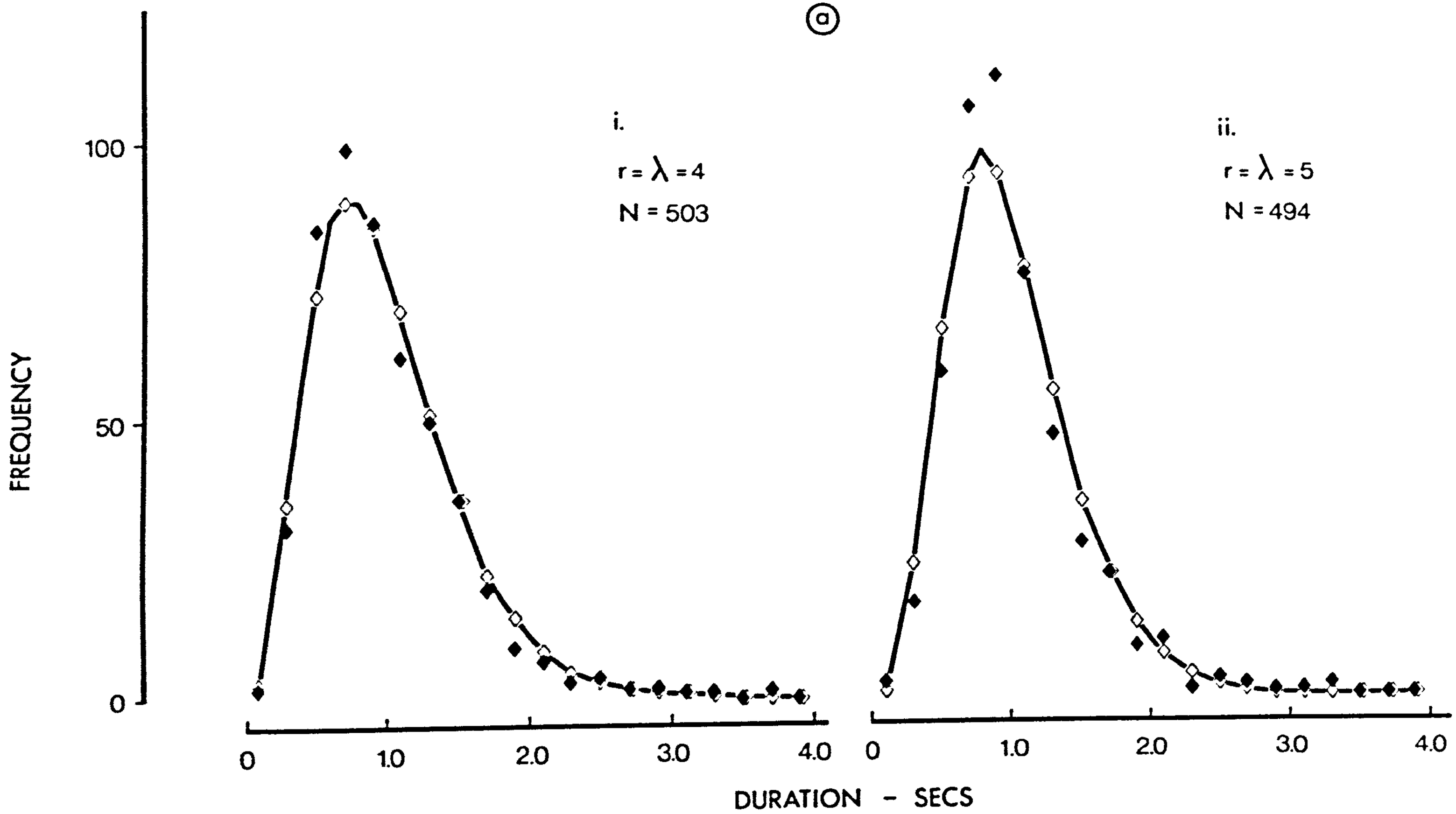
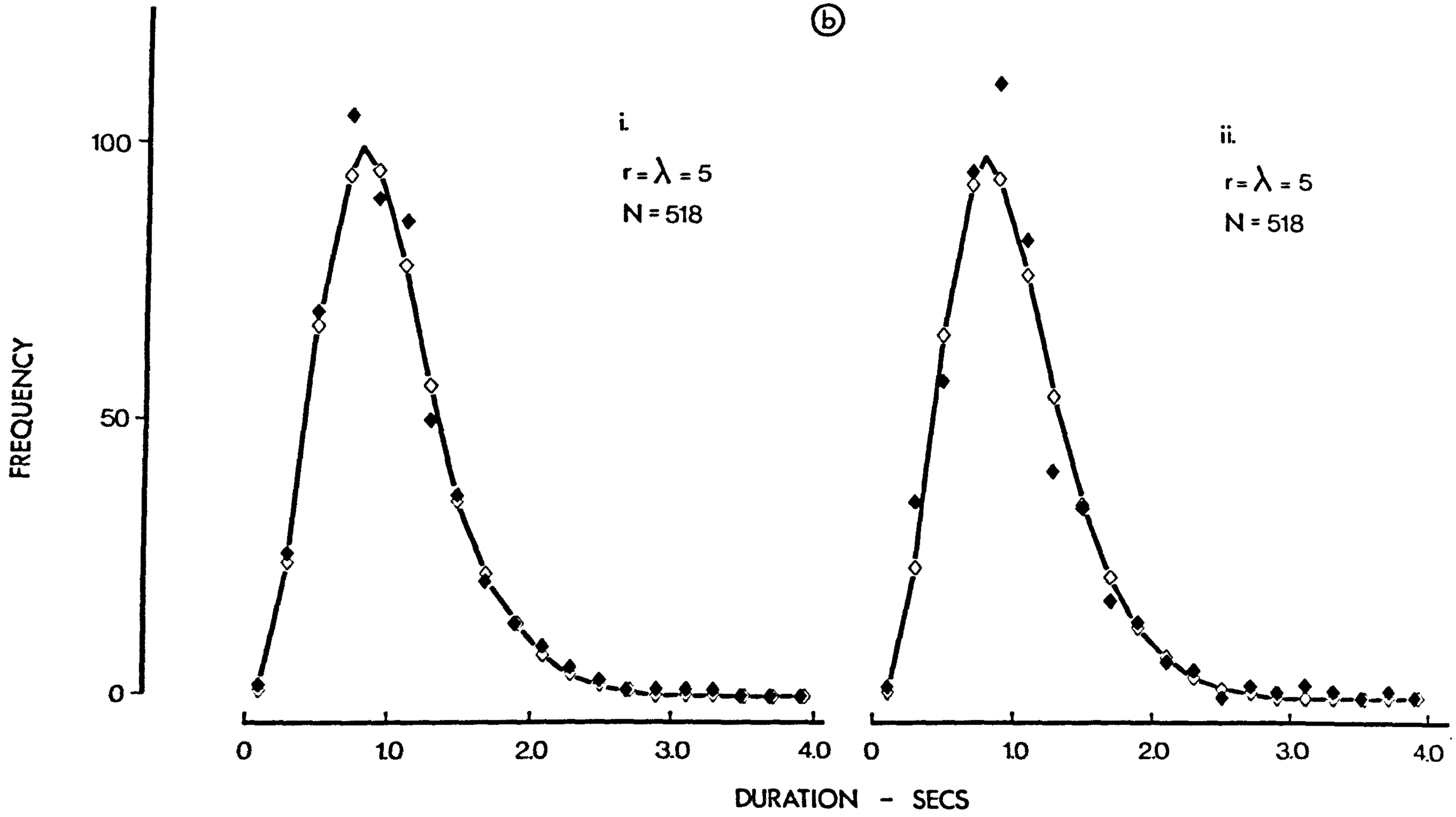

c
b
a
1.0
0.6
0.2
0.0
0.2
1 2 3 4 5
LAGS
MEAN AUTOCORRELATION COEFFICIENTS

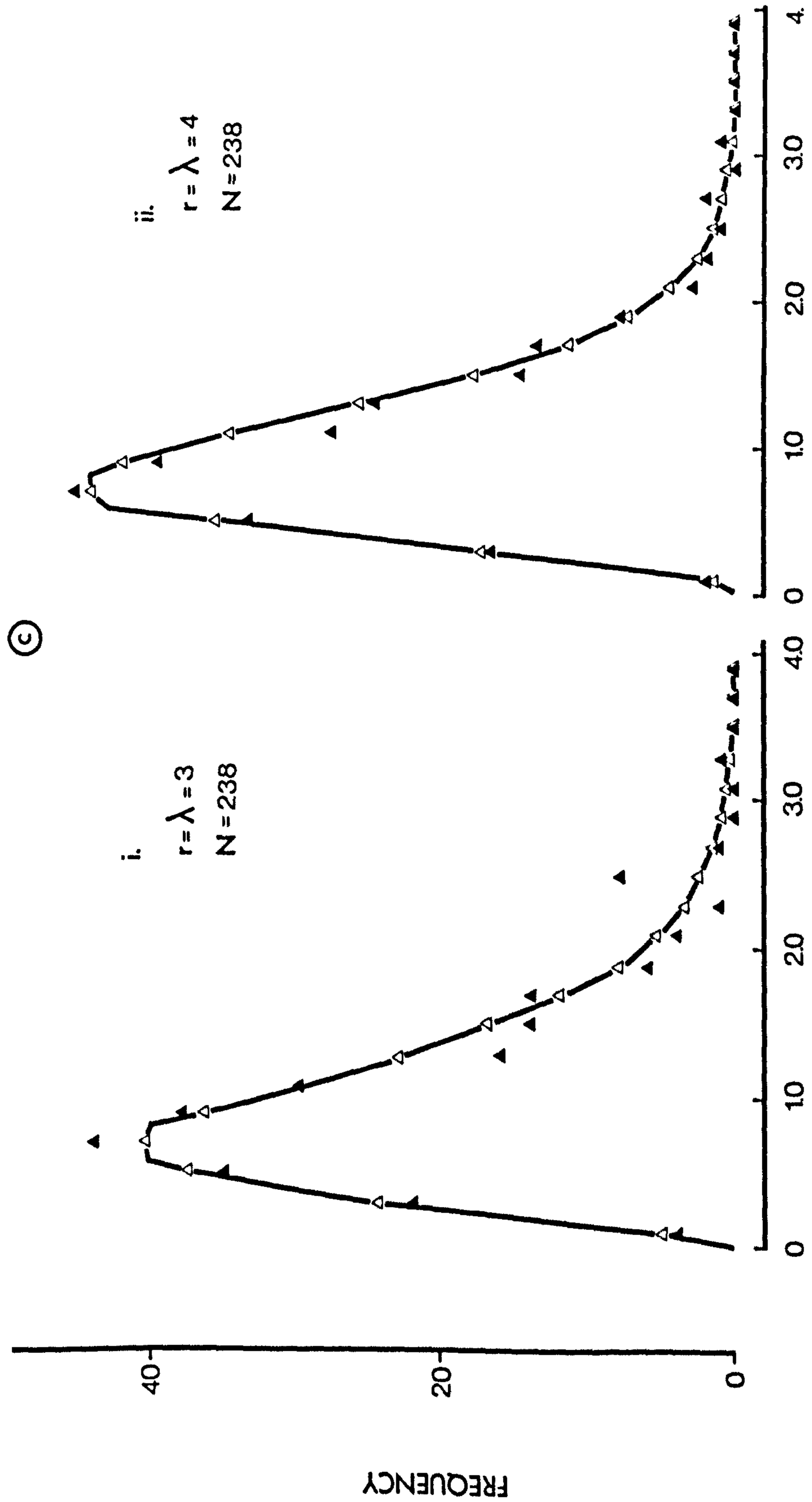
Figure 21

◆-- ▲--, the observed frequencies, combined over subjects, associated with the different phase durations, are compared with the frequencies generated by the gamma distribution, ◇-- △--, having the values indicated for r and λ .
a and b, chromatic stimuli, with i and ii corresponding to the dominance phases of the red and green fields, respectively. b, replicate data.
c, achromatic stimuli, with i and ii corresponding to the dominance phases of the vertical and horizontal gratings.

(a)


i.
r = λ = 4
N = 503
ii.
r = λ = 5
N = 494
100
50
0
FREQUENCY
0
1.0
2.0
3.0
4.0
DURATION - SECS


(b)
i.
r = λ = 5
N = 518
ii.
r = λ = 5
N = 518
FREQUENCY
100
50
0
0
1.0
2.0
3.0
4.0
DURATION - SECS


ii.
r = λ = 4
N = 238
4.
3.0
2.0
1.0
0
DURATION — SECS
(c)
i.
r = λ = 3
N = 238
4.0
3.0
2.0
1.0
0
40
20
0
FREQUENCY

RESULTS AND ANALYSIS

Although the data concerning the achromatic and chromatic stimuli are presented together, the former receive separate consideration at the end of this section.

Chromatic Stimuli

With each subject contributing data from two equivalent trials in the first experiment, it was possible to have a replication of each test. As a preliminary to the tests of sequential dependency, the relationship between the standard deviation and mean for the dominance phase durations was expressed as a regression coefficient, and, in accordance with previous findings (Levelt, 1966), a strong positive linear relationship was evident in every case, cf. Table 26. In addition, for each rivalling field, a regression analysis was undertaken to detect temporal linear trends. For this purpose, successive phases of dominance were labelled 1, 2, 3 ... and the corresponding durations were regressed on these values. Regression coefficients were determined for each subject together with the associated F values. Presented in Table 27 are the average values obtained for the slopes of the regression lines, and for the associated F values. As can be seen from the table, no significant temporal trends were in evidence.

Several different tests of dependency across successive phases of the rivalry alternations were undertaken.

(1) As a first measure of sequential dependency, the average absolute slope of successive durations (a test of first-order dependencies, cf. Lathrop, 1966) was determined for the red, green, and combined red/green sequences. The formula employed in computation was:

$$L_j = \sqrt{\sum_{i=1}^{N-1} \frac{|X_{(i+1)j} - X_{ij}|}{(N-1)\sigma}}$$

where L_j = the value of the statistic for the j-th sequence, X_{ij}, $X_{(i+1)}$= successive responses in the j-th sequence, σ = the within js standard deviation.

An analysis combining the red and green phases was made possible with a tranformation of the data involving the division of each dominance duration by the mean duration for that field on that trial. This transformation also permitted the data from the different subjects to be later combined.

The expected value for this measure, when successive phase durations are independent, is 1.0, with an associated standard deviation of $1/2\sqrt{N}$. A positive relation across successive durations (indicating a stable series) would be reflected in values lower than the expected. Higher values would be indicative of an alternating series.

With the statistic following a normal distribution it was possible to determine a z score for each of the obtained values. Table 28 gives the average values for the Lathrop statistic and for the corresponding z scores. Combining the two sets of data, the average values obtained for the Lathrop statistic can be seen to be very close to those predicted under the assumption of sequential independence (0.9993 for the combined red/green sequence, 0.9933 for the red, and 0.9919 for the green sequences). Analysis of the chi-squared type on the obtained z values failed to reveal a significant heterogeneity among these values for any set of sequences and tests involving the conversion of $\sum z$

to a unit normal deviate value failed to assign significance to any of the overall deviations from zero. In conclusion, therefore, an analysis based on the Lathrop statistic failed to provide evidence for a sequential dependence within the sequences of rivalry alternations.

(2) Treating the rivalry phase durations as successive values in a time series, an analysis of the type described by Kendall (cf. Kendall, 1973, chapter 2, pp. 21 onwards) was undertaken. One advantage of this analysis over the Lathrop statistic relates to the fact that the expected values have been theoretically, as opposed to empirically determined. Other advantages accrue from its nonparametric nature.

(a) Number of turning points analysis. Defining a turning point as a point in a time series whose associated value has neighbouring values less than it (defining a peak) or greater than it (defining a trough), then for a series of n values, the expected number of turning points under the assumption of independence of successive values is $(2/3)(n-2)$, and the expected variance of this parameter is then given by $(16n-29)/90$. With the number of turning points following a normal distribution, each observed value was converted to a z score.

An oscillating or rapidly fluctuating series would reflect itself in more turning points than anticipated, while a series tending toward stationarity (successive values being positively correlated) would reflect itself in fewer such points. Thus, the number of turning points was determined for the series from each trial, separately for the exclusively red, the exclusively green and the combined red/green sequences.

Given in Table 29 are the average values for the z scores associated with the number of turning points observed in each sequence. Analyses of the chi-squared type on the

obtained z values failed to reveal a significant heterogeneity among any set of values, and tests involving the conversion of $\sum z$ to a unit normal deviate value failed to assign significance to any of the overall deviations from zero. It may be concluded from these results that the sequential dependence hypothesis obtained no support from the data.

(b) Phase length analysis. Since it is of some interest to consider not just the number of turning points but the distribution of intervals between them, a second related test was performed on the distribution of phase lengths (cf. Wallis and Moore, 1941). The parts of a time series between successive turning points are referred to as phases (the first and last, incomplete phases are ignored in the analysis), with lengths defined as the number of points spanning a phase, inclusive of the two turning points, less one. Under the assumption of sequential independence, the expected number of phases of length d in a series of total length n, is then

$$\frac{2(n-d-2)(d^2+3d+1)}{(d+3)!}$$

A chi-squared test, modified to accommodate the nonindependence of phase lengths from the same series (cf. Wallis and Moore, 1941) was employed to assess the significance of the observed deviations from the expected frequencies.

Table 30 gives the average observed frequencies for the different lengths of phases (phase lengths of 3 and over being pooled) together with the average expected values. The associated values for chi squared are also tabled, these values being derived from the "total" frequencies, obtained by adding the results across subjects. As can be seen from the table, the observed frequencies failed to deviate significantly from those expected on the assumption of independence.

(3) In order to assess the effects of increasing the separation between "successive" phase durations, an autocorrelation analysis was performed, through lag 5. Apart from revealing the effects of temporal separation, such an analysis, unlike the preceding ones, allows the correlation between successive red and preceding green phases to be separately considered from that between successive green and preceding red. The following four phase relations could therefore be considered: (a) red with preceding green, (b) green with preceding red, (c) red with preceding red, and (d) green with preceding green.

Given in Table 31 are the average values obtained for the autocorrelation coefficients for each of the four possibilities. Figure 20 illustrates the same data in the form of correlograms, with the inclusion of the mean standard deviation associated with these averages (the vertical bars delineate the range of values spanned by two standard deviations, symmetrically placed about the zero level).

After what would be an initial coefficient of 1.0 for lag zero, the coefficients can be seen to be of small magnitude, reflecting the absence of any sequential dependence.

Inspection of the correlograms suggests, however (though for the "original" data only), the existence of a downward trend across successive lags. Formal tests (cf. Jonckheere and Bower, 1967) assigned significance to these trends for all four phase relations in the original data (the associated z scores being 2.259, 3.28, 1.66, and 1.66 for the correlations a to b, respectively), though for none in the replicate data (the z scores in this case being -0.98, 0.98, 1.57, and 0.725). However, in view of the considerable individual differences in trend that were present, it is unfortunate that formal tests for heterogeneity were

precluded by the rather short nature (only five values) of the protocols. As Jonckheere and Bower point out, the chi-squared test suggested for this purpose is really only applicable where the individual protocols involve at least 10 values. Moreover, although the trends in the one set of data are statistically significant, it must be remembered that correlation coefficients of this order attribute only a very small portion of the total variance to the correlation (cf. Hays, 1963, p 502, who points out that a correlation coefficient of 0.15, say, could be interpreted as attributing only 2.25% of the total variance to a linear correlation). Together with the complete absence of such trends in the replicate data, it would seem that whatever processes underly the consistent behaviour, across successive lags, of the autocorrelation coefficients, they do not contribute "significantly" to the occurrence or temporal course of binocular rivalry.

(4) Finally, the frequency distributions of the rivalry phase durations were compared with a theoretical frequency distribution. For this purpose, the values for the phase durations were converted to histogram form, being assigned to intervals of 0.2 sec. width.

In Figure 21 the frequency values for thephase durations, combined over subjects, are compared with the frequencies generated by the two-parameter gamma distribution:

$$f(x) = \frac{\lambda^r}{(r-1)!} \cdot x^{r-1} \cdot e^{-\lambda x}$$

As mentioned above, to establish a common baseline across subjects, the individual dominance phase durations of a field were divided by the mean duration for that field on that trial. Such a procedure obtains a mean equal to 1.0.

The mean and variance of the pooled frequency distributions were used to estimate the parameters r and λ, on the basis of the relationships:

$$\lambda = x/\sigma^2 \text{ and } r = x^2/\sigma^2$$

The computed value for r was rounded off to the nearest integer before being used in the gamma function.

The graphic fit of the frequency distributions can be seen to be close, indicating again that successive rivalry phase durations are independent. Moreover, the actual values obtained for r and λ are directly comparable to those obtained in previous studies (Blake et al, 1971; Fox and Herrmann, 1967; Levelt, 1966). The significance of this striking correspondence is difficult to interpret.

Achromatic Stimuli

As can be seen from Tables 26-31, similar conclusions may be drawn concerning the achromatic stimuli, that is, regarding the alternation process between the differently oriented square-wave gratings. There was again the strong positive linear relationship between the standard deviation and mean value for the dominance phase durations, together with an absence of temporal trends across successive phases.

The Lathrop statistic failed to attach significance to the results and the same story held for the number of turning points analysis. From Table 30 it can be seen that the analysis based on the phase lengths similarly failed to yield significant results. The autocorrelation analysis, cf. Table 31, yielded small insignificant average values, with perhaps the one exception of the autocorrelation of vertical with preceding horizontal phases, for lag 1. Finally, inspection of Figure 21 indicates that the two-parameter gamma function again described reasonably well

the frequency distribution of the rivalry phase durations, for both stimulus fields.

In summary, therefore, it would seem justifiable to conclude, as with chromatic stimuli, that whatever processes might give rise to a statistical dependence across successive phase durations in rivalry, they do not contribute significantly to the occurrence or temporal course of rivalry.

DISCUSSION

For none of the several tests employed was there evidence to suggest that successive binocular rivalry phases are dependent, for either achromatic or chromatic stimuli. Moreover, for both types of stimuli a gamma distribution described the frequency distribution of the rivalry phase durations. It is confirmed therefore, that the stochastic properties of the perceptual alternations are similar in the cases of binocular rivalry and reversal of ambiguous figures. Whilst not proof, this correspondence suggests that similar processes underly the two phenomena and that, therefore, the processes underlying rivalry are more fundamental than is traditionally thought, and not at all restricted to conditions that involve the separate presentation of different stimuli to the two eyes. This is consistent with the model outlined above.

On the basis of the observed independence of successive phase durations, it is tempting to reject explanations of the rivalry process (cf. Chapter 2) that hold that the alternations arise from the adaptation toward the currently dominant stimulus, and the recovery from adaptation toward the non-dominant stimulus (the traditional explanation of the reversal of ambiguous figures, cf. Orbach, Erlich and Heath, 1963), since, for example, longer periods of red dominance may then be expected to be succeeded by longer periods of green dominance. However, though the relevance of such a model is clearly made doubtful with the stochastic properties, a number of additional postulates need to be incorporated before such a model could begin to describe the rivalry process. Thus, for example, adaptation may be assigned a much more indirect role in a model that accommodates the property of sequential independence, as Taylor and Aldridge (1974) have outlined with reference to the alternation of ambiguous figures.

Finally, insofar as the stochastic properties of the rivalry observed in Experiment 1 correspond with those described by other researchers, using different stimuli, it is clear that subjects were reliable in reporting the rivalry alternations between the red and green homogeneous fields.

Conclusion

In conclusion, we may say that the stochastic properties of the rivalry alternations indicate that the processes underlying the alternations, which are perhaps the most difficult to pin-down, may contribute to perception in other contexts. In turn, this helps confirm the hypothesis, incorporated in the outline model of perception and attention of Chapter 4, that the processes responsible for rivalry are relatively fundamental, and not confined to conditions that involve the separate presentation of different stimuli to the two eyes. Furthermore, these results help justify the analogy, drawn in Chapter 4, between binocular rivalry and ambiguous figures in terms of the mutually exclusive nature of perception in the two contexts.

CHAPTER 6 THE PERCEPTUAL FRAGMENTATION OF UNSTABILIZED IMAGES

The exclusive nature of rivalry, and the stochastic properties of the alternations, highlight the similarities with the perceptual reversal of ambiguous figures. These similarities suggest that the same fundamental processes are involved in the two phenomena.

The disappearance (suppression) of the monocular images is an additional aspect of rivalry that may generalize to other perceptual phenomena and thereby confirm the notion that the processes responsible for rivalry are not specific to situations that involve the separate presentation of different stimuli to the two eyes. It will be instructive then, to ask if there are other situations in which stimuli disappear in a manner that is characteristic of rivalling images.

It is well known that visual stimuli fragment and occasionally disappear completely when viewed under conditions that eliminate the effects of small involuntary eye movements (Bennet-Clark and Evans, 1963; Heckenmueller, 1965; Pritchard, Heron and Hebb, 1960), and for several reasons (to be discussed more fully below) one may expect the behaviour of such stabilized images to reflect something of the processes underlying the suppression in binocular rivalry. Before determining whether a parallel exists between the behaviour of stabilized and rivalling images, however, it must be appreciated that such a parallel would contradict the traditional explanation of the former phenomenon. Whilst, traditionally, it is held that the disappearance of stabilized images reflects underlying processes of adaptation, we have seen that it is a process of habituation that is more likely to be involved in the disappearance of rivalling images. Thus, if stimuli were found to behave in a corresponding manner in the two contexts, either the traditional explanation of the disappearance of stabilized images would be questioned, or the view that

rivalry suppression reflects habituation would have to be abandoned. For the present thesis, then, it is important that recent evidence has questioned the appropriateness of adaptation as it is applied to the disappearance of stabilized images. Thus, not only does the structured or meaningful nature of the fragmentation indicate that central processes are involved (Pritchard, Heron and Hebb, 1960; Evans, 1965; Evans and Wells, 1967; Davies, 1973) but the elimination of the effects of small involuntary eye movements is not a prerequisite for the occurrence of fragmentation (Donderi and Kane, 1965; Evans and Piggins, 1963; Evans, 1973; MacKinnon, Forde and Piggins, 1969; McKinney, 1963; Piggins, 1970).

In order to demonstrate that the disappearance of images is an additional aspect of rivalry that is not specific to situations that involve the separate presentation of different stimuli to the two eyes, an attempt was made to replicate, in rivalry, some observations that are typically associated with stabilized images.

PROCEDURES

The same procedure was common to the four experiments that follow. Subjects reported the changing appearance of a number of stimuli under particular viewing conditions. In no case were attempts made to compensate the effects of small involuntary eye movements; subjects were simply asked to relax and steadily fixate some central part of the stimulus.

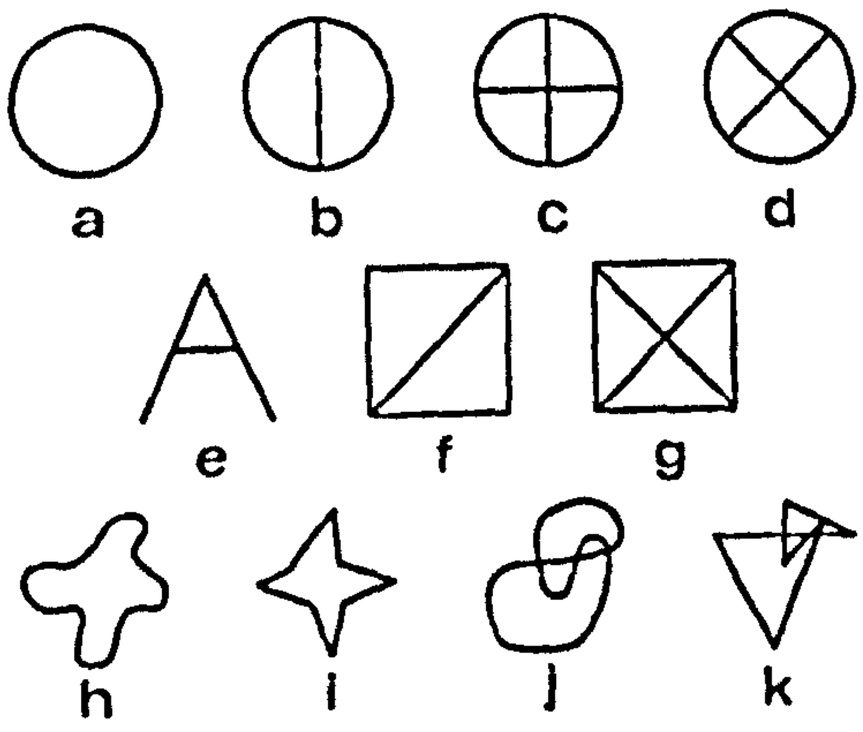
A series of practice trials was allowed each subject, during which the different stimuli were presented, in turn, for 60 seconds. The fragmentation of each figure was reported by the alternate closure of two switches; the first (left hand) whilst the figure appeared partially or totally suppressed, and the second (right hand) whilst the figure remained intact. For the experimental session, an order of presentation was randomly determined for each subject. Each of these trials lasted 60 seconds, and was followed by a 60-second rest period during which the number of times, and the total durations for which, each switch had been closed were recorded.

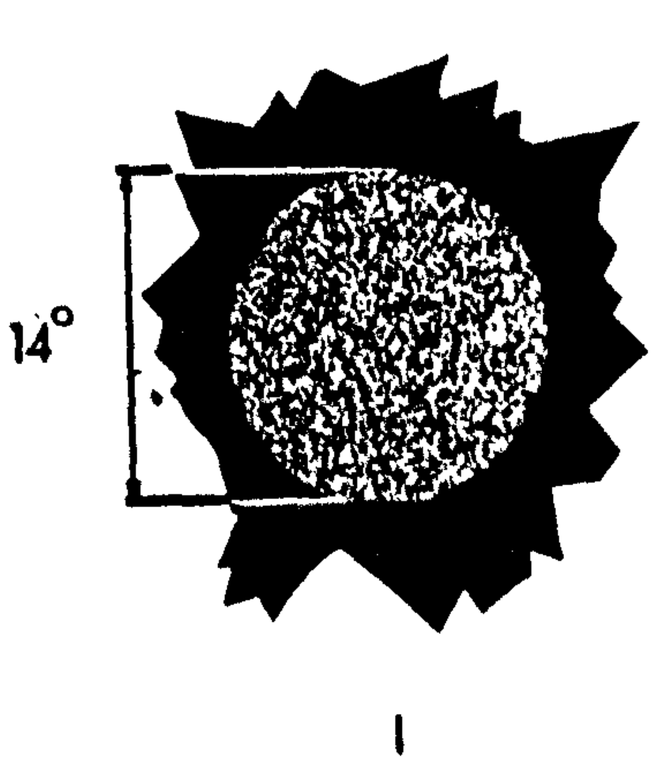
SUBJECTS

Twenty-nine undergraduate students, from departments other than psychology, served as subjects in the experiments. The subjects involved in Experiment 9 included a pilot subject who was experienced in observing phenomena associated with binocular rivalry.

Figure 22

The stimuli, a-k, presented to a subject's left eye, and positioned to appear within the quasi-random field, l, that was presented to his right eye.





l

6.1 Binocular Rivalry

EXPERIMENT 9 IMAGE FRAGMENTATION IN BINOCULAR RIVALRY

Thirteen subjects reported the changing appearance of a number of different stimuli during binocular rivalry. These stimuli, a-g, together with the quasi-random pattern, 1, that was presented to the contralateral eye, are illustrated in Figure 22. Each of the patterns a-c and e-g was presented to each experimental subject on four trials. A pilot subject received each of the stimulus patterns a-g on 10 trials.

Apparatus and Materials

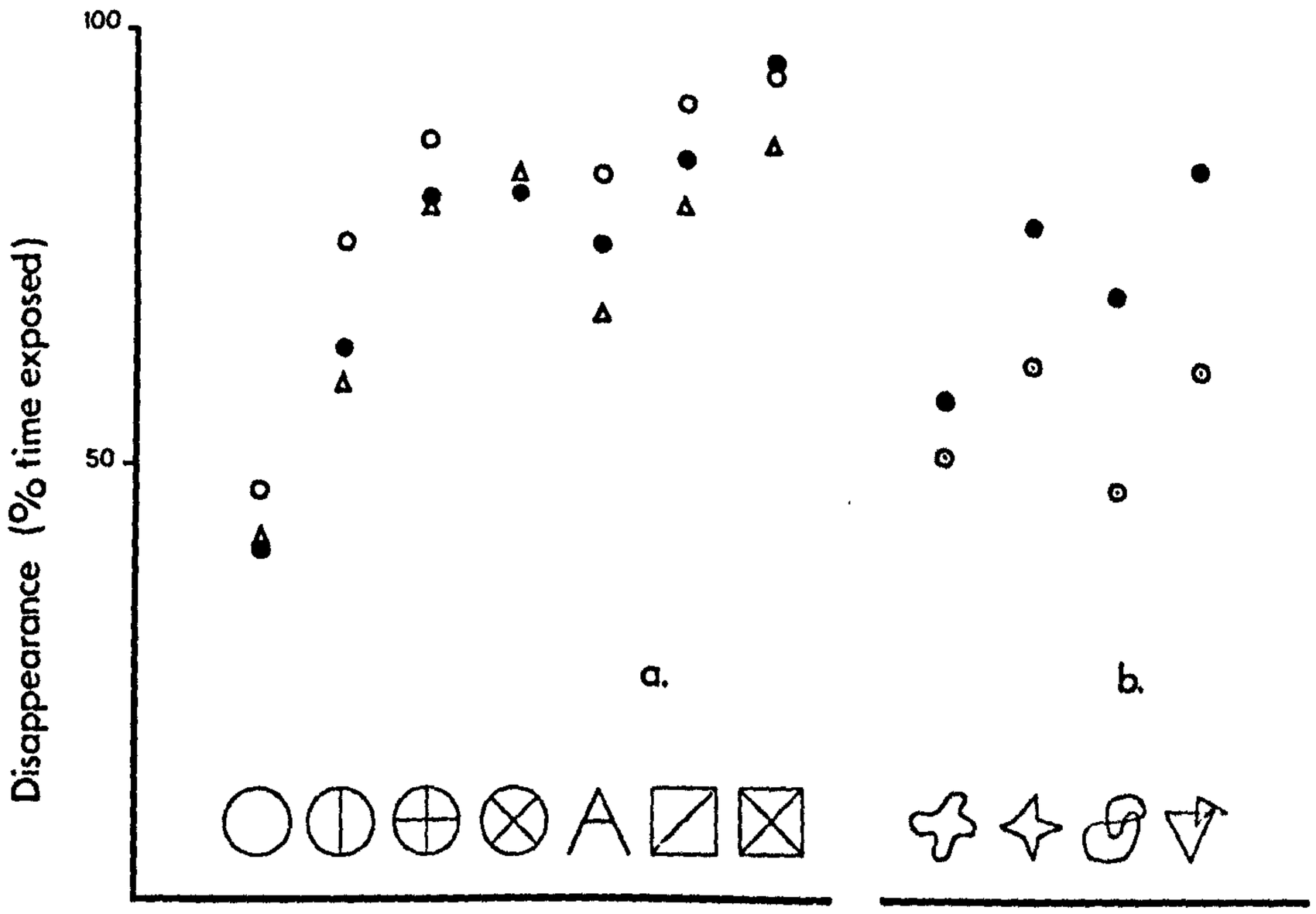
The stimuli, in the form of black/white photographs, were presented in the circular fields of the stereoscope that was employed in Experiment 1. These fields subtended 14 degrees, and, as in Experiment 1, were transilluminated by a small flourescent striplite that was positioned behind and above the stereoscope. A diffusing screen was placed between the lamp and the two fields. No ancillary equipment was employed that would serve to eliminate the effects of involuntary eye movements. Rather, subjects simply relaxed and steadily fixated some central part of the stimulus display.

Stimuli were selected for which quantitative data were available regarding their mode of fragmentation during stabilized viewing (cf Evans, 1965). Figures a-k were photographed from Evans (1965) and the reproductions were placed in the left field of the stereoscope. In their maximum dimension the figures subtended approximately 6

degrees, and the lines were 11 min. in width. A similar photographic reproduction of commercially available Letratone (pattern LT 100) was presented to the contralateral eye (cf. Figure 22). The luminance of the lighter parts of each field was fixed at approximately 0.9 log ft. lamberts.

Figure 23

The average values for the percentage of total viewing time for which subjects reported the partial or total suppression of the patterns a-k.
Data from a previous report reflecting the behaviour of the figures as stabilized images, ●.
(a) Data from a pilot subject, △, and a group of 12 subjects, ○, obtained in the binocular rivalry conditions of Experiment 9. Each △ point represents the average of 10 values, and each ○ point the average of 48 values.
(b) Data from five subjects who viewed the patterns h-k under the binocular rivalry conditions of Experiment 10. Each ⊙ point represents the average of 15 values.


100
50
Disappearance (% time exposed)
a.
b.

RESULTS AND ANALYSIS

All subjects reported the ready replacement of the figures a-k, either in whole or part, by the contralateral random pattern. There was general agreement among subjects that the fragmentation was not totally random or haphazard; rather, there was a tendency for the different components of the figures (circles, bars and crosses) to behave in a unitary manner. Thus, with figure c it was occasionally reported that just the circle disappeared, leaving the inscribed cross intact. Evans's illustration of the typical structured fragmentations that arise with the stabilized viewing of figure c (op. cit., Fig. 8, p. 130) appears to be descriptive of the subjects' reports in the present study.

Figure 23(a) shows the average values for the percentage of total viewing time for which subjects reported patterns a-g to be partially or totally suppressed. Plotted separately are the results from the group of twelve subjects, and the results from the pilot subject. For comparison, Figure 23(a) also presents the averaged values from Evans's data concerning the fragmentation of the same stimuli when viewed as stabilized images (op.cit., Fig. 3, p.124).

Though the correspondence in behaviour of the patterns across the two conditions is clear from inspection of Figure 23(a), a test derived from Kendall's rank correlation methods (Kendall, 1955) assigned formal significance to the results. The pilot subject's data (excepting those for figure d) were included in the test that was undertaken on the mean subject by figure scores. A statistic was determined for each subject's results to indicate the degree of correlation with Evans's data. More specifically, the value of the statistic R is given by the number of occasions on which the difference between a pair of mean values in a subject's results lies in the same direction as the corresponding difference in the reference data.

In this way, a value for R was obtained for each subject, and these were later combined to give a Z score in the following way:

$$Z = \frac{\sum R - \frac{1}{2} - \frac{1}{4}mn(n-1)}{\sqrt{\frac{mn(n-1)(2n+5)}{72}}}$$

where m = the number of subjects (13);

n = the number of mean values in each subject's results (6),

$\frac{1}{2}$ = the correction for continuity;

$\frac{1}{4}mn(n-1)$ = the expected value of $\sum R$ under the assumption of an equal probability of occurrence of every possible arrangement of the results

$\sqrt{\frac{mn(n-1)(2n-5)}{72}}$ = the standard error of $\sum R$

Indicative of a highly significant positive correlation with Evans's data, values of 153 and 5.73 were obtained for $\sum R$ and Z respectively ($P < 0.01$).

EXPERIMENT 10 THE EFFECT OF STIMULUS ANGULARITY ON THE FRAGMENTATION OF RIVALLING IMAGES

With field brightness, width of line, contrast and overall retinal projection area held constant across stimuli a-g, Evans considered that readiness to fragment was a function of the presence of "angles". His demonstration with stimuli h-k that angular figures disappear more readily than their curved counterparts reinforced this belief. Moreover, as Evans (1965) points out, the total amount of contour in a stimulus appears to be an unimportant factor. Whilst stimulus e has a consistently higher percentage of disappearance than stimulus a, the amount of contour that it involves is actually less. On the basis of the results from Experiment 9 it was predicted that angularity would have similar implications for suppression in binocular rivalry.

Each of five subjects was presented with reproductions of stimuli h-k in the manner of the first experiment, with the exception that there were just three presentations of each pattern.

RESULTS AND ANALYSIS

Again subjects reported that the figures were readily replaced by the contralateral pattern. The mean values for the percentage of total viewing time for which figures h-k were suppressed (partially or totally) are illustrated in Figure 23(b), together with the corresponding information from Evans (op.cit., Fig. 5, p.126). The correspondence in

the behaviour of the patterns across the rivalry and stabilized viewing conditions is again significant. When reference is made to the raw data from which these means are derived, a comparison of the within subject values for figures h and j with the corresponding values for figures i and k (where corresponding is defined by the temporal proximity of the trials) reveals only three out of a possible thirty contrasts that run counter to the predictions.

DISCUSSION

Whilst similar perceptual effects need not derive from the same mechanism(s), it would appear likely, on the basis of these two experiments, that the processes involved in the suppression in binocular rivalry contribute to the disappearance and fragmentation of stabilized images. The notion that the processes underlying binocular rivalry are not specific to conditions that involve the separate presentation of different stimuli to the two eyes is supported. Conversely, the data add weight to the case against explanations of the behaviour of stabilized images that rely upon processes of adaptation.

6.2 Monocular Rivalry

The exclusive nature of rivalry, the perceptual alternations and the suppression that it involves, reveal themselves in contexts that do not involve presenting different stimuli to the two eyes. This is consistent with the theoretical framework outlined in Chapter 4, which does not attach critical importance to the dichoptic presentation of the stimuli. The scheme also suggests that it should be possible to imitate all three features of rivalry in a situation where all visual information is either presented to just one, or to both eyes. In other words, these data and the theoretical scheme indicate that it should be possible to have monocular rivalry. There is preliminary evidence to confirm this.

Breese (1899) simultaneously presented a red and green square to one eye. Superimposed on these squares were obliquely oriented series of parallel lines, that were orthogonally oriented for the two colours. He observed the occurrence of a form of rivalry between the two images, wherein first one, and then the other square appeared much clearer and in the foreground. The lines accompanied their squares, and Breese reports that these occasionally disappeared.

Honisett and Oldfield (1961) had subjects steadily fixate the centre of various displays under normal (not dichoptic) viewing conditions, and when a grid pattern was used their subjects reported that the horizontal and vertical lines would occasionally disappear. Rather than relate this to the fragmentation of stabilized images, Honisett and Oldfield drew a parallel with binocular rivalry.

Sindermann and Luddeke (1971) followed the 40 sec. presentation of a white vertical bar on a black ground, with the presentation of a horizontal black bar on a white card. As a result, subjects perceived the negative

(black) afterimage of the vertical bar together with the real image of the horizontal bar so that if both had been simultaneously visible, a black cross would have been formed. The effect was that with the alternating dominance of the two images, the non-dominant image suffered suppression near the borders of intersection with the other bar. Sindermann and Luddeke focused on the extent of the "halo effect" as it affected the vertical bar and as it varied with the width of this bar. The same procedure was undertaken with respect to binocular rivalry, when the afterimage and real image originated in different eyes. The same quantitative relationship between the two variables was obtained in the two contexts, confirming that the behaviour of the images in the former condition was a true analogue of binocular rivalry.

Finally, Campbell and Howell (1972) and Campbell, Gilinsly, Howell, Riggs and Atkinson (1973) superimposed a red and a green sinusoidal grating, at different orientations, and observed a monocular rivalry between the two, in which first one and then the other grating emerged as the figure, whilst the other receded in to the ground.

This preliminary evidence suggests that, consistent with the theorectical framework outlined above, it is possible to imitate binocular rivalry under "monocular" viewing conditions i.e. where both rivalling stimuli are presented to the same eye(s). Apart from the experiment of Sindermann and Luddeke, however, the similarities between the two contexts have been drawn at a superficial level. Moreover, since these reports indicate that a stimulus is unlikely to disappear completely in monocular rivalry, we may be justified in treating the phenomena as special cases of the alternation of ambiguous figures. In the following experiment, therefore, an attempt was made to replicate the findings of the previous two experiments in the context of monocular rivalry. Thus, it was asked whether

stimuli would behave in monocular rivalry in a manner corresponding with their behaviour in binocular rivalry and stabilized imagery.

EXPERIMENT 11 IMAGE FRAGMENTATION IN MONOCULAR RIVALRY

Six subjects reported the changing appearance of stimuli that were viewed under normal (not dichoptic) conditions. Thus, subjects relaxed in an armchair and viewed, from a distance of 2.5 metres, a screen upon which each one of the patterns illustrated in Figure 24 was projected, in a randomized order, on three separate trials. It was arranged that these figures should be projected in red light and be superimposed on the quasi-random pattern whilst this was projected in green light. Again no attempt was made to compensate for involuntary eye movements, rather, with an unobstructed view of the screen, each subject was instructed to relax and steadily fixate some central part of the stimulus display.

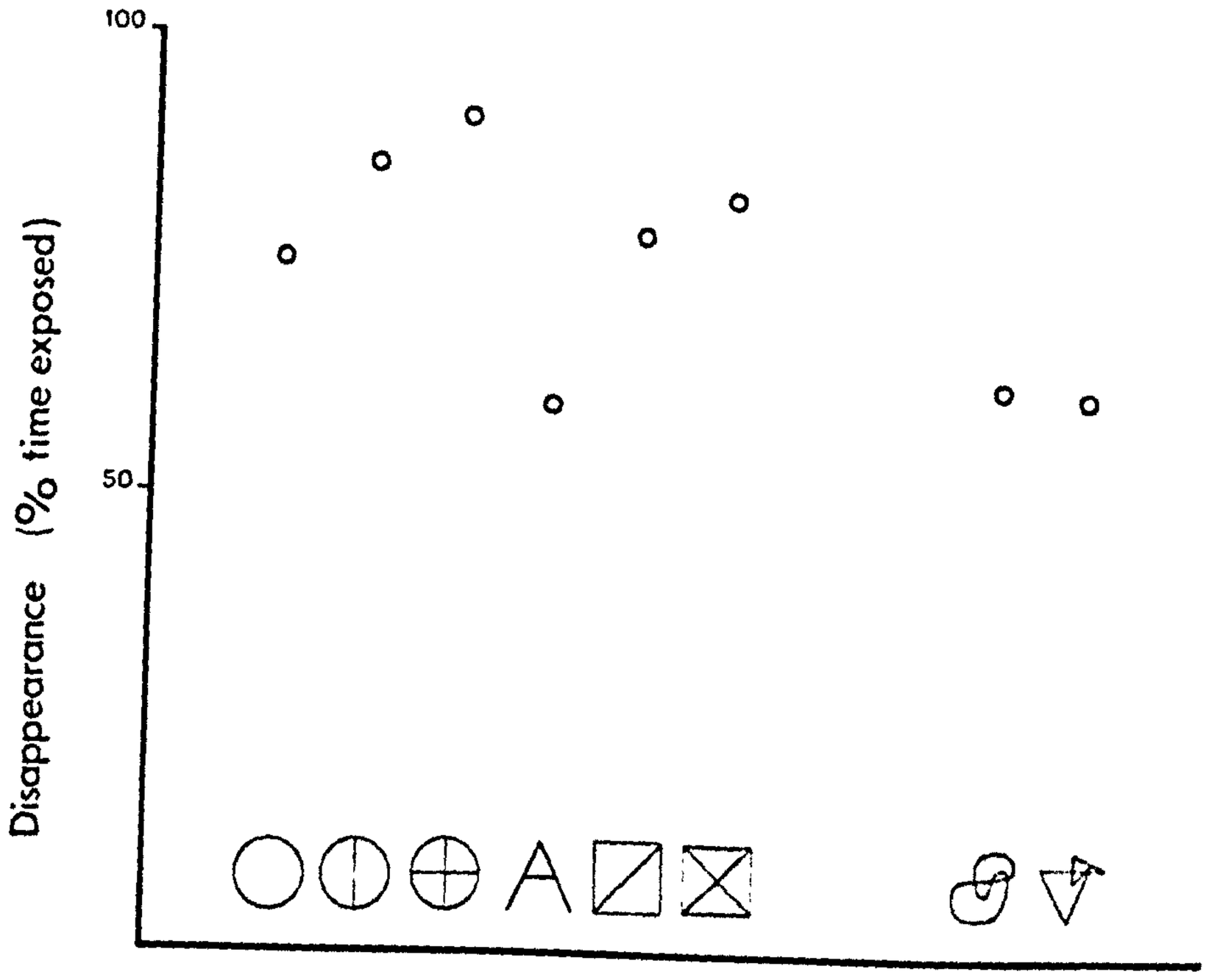
Apparatus and Materials

Slides were made of the photographic negatives of stimuli a-k and of the quasi-random field (cf Fig. 22). The first of two Aldis Tutor 1000 projectors (lamp; Philips M9, 300w., A1/178) was used to project the quasi-random pattern on to a light grey screen. Immediately in front of the projector was placed a standard green filter (Ilford 625). The second projector was positioned so that

images of the patterns a-k could be superimposed on the centre of the random field. Before this projector was placed a standard red filter (Ilford 205). Viewed from a distance of 2.5 metres, each side of the random field (this now being square in overall shape instead of circular), and each of the stimuli a-k, subtended 9.33 and 6.00 degrees respectively. In their width, each of the lines comprising the latter stimuli subtended a visual angle of 11 min. The luminance of the lighter parts of the stimuli upon projection was measured at 1.7 log ft. lamberts (50.7 cd/m^2). The two projectors were the only sources of illumination in the experimental cubicle.

Figure 24

Results from the monocular rivalry condition of Experiment 11; each point representing the average of 18 values.


100
50
(% time exposed)
Disappearance

RESULTS AND ANALYSIS

For all subjects the red figures readily disappeared. When invisible, they did not distort the colour of the random green field upon which they were superimposed, nor did they leave any other trace of their existence.

Illustrated in Figure 24 are the average values for the percentage of total viewing time for which subjects reported the different patterns to be partially or totally suppressed. Though there is a close correspondence with the values illustrated in Figure 23 (a correlation analysis assigns a value of 6.67 to Z, $P<0.01$), a discrepancy does exist. More specifically, the results of an analysis of variance for repeated measures does not confirm the greater stability of figure j over k, and of the group of figures a-c (those involving the circle) over the group e-g. Indeed, the situation appears reversed, though not significantly so ($F=5.3$, where the critical value, for an unplanned comparison at $P<0.05$, is 15.75). The results from a further study demonstrated that this discrepancy arose from the change in overall shape of the random field.

EXPERIMENT 12 THE EFFECT OF THE FIELD BOUNDARY ON THE FRAGMENTATION OF IMAGES

Under the conditions of Experiment 11, each of five subjects viewed, and reported on, the fragmentation of figures a, e, j and k, whilst these were superimposed on a randomly textured field that was either square or circular in overall shape. An additional slide was constructed so that in the latter case the random field subtended 10.68 degrees.

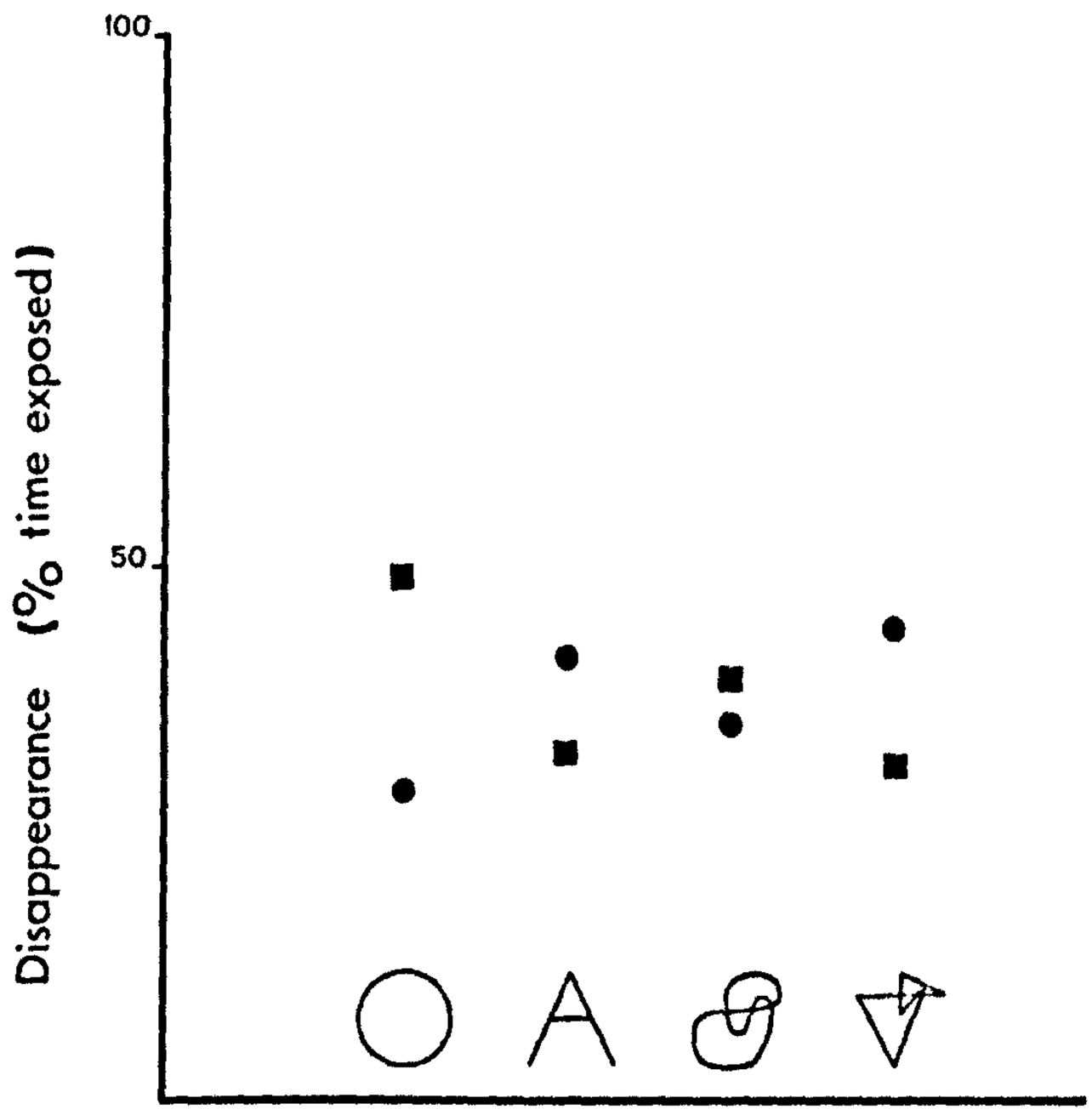
RESULTS AND ANALYSIS

The quantitative results are illustrated in Figure 25. Whilst figures a and j can be seen to be relatively more stable than their counterparts when viewed against the circular random field, the opposite is the case in the context of the square field. A repeated measures analysis of variance revealed this interaction to be significant ($F=11.81$, $df=1,28$, $P<0.005$). It would appear, therefore, that angular figures disappear more readily than curved figures only in the context of a curved or circular field. The results therefore add a cautionary note to Evans's interpretation of his own results regarding "angularity", since his targets were viewed within a circular field.

With the discrepancy of Experiment 11 thus resolved, it may be concluded that figures a-k behave in a similar manner in monocular and binocular rivalry, and in stabilized viewing.

Figure 25

Data from the monocular rivalry condition of Experiment 12. Each point represents the average of five values; the stimuli being viewed against a field that was either square (■) or circular (●) in overall shape.


Disappearance (% time exposed)
100
50

DISCUSSION

Whilst similar perceptual effects need not derive from the same mechanism(s), and though only a limited number of stimuli have been employed, the reproduction of typical stabilized image effects in binocular and monocular rivalry does suggest that common processes are involved. This is consistent with the theory outlined in Chapter 4, which incorporates the notion that the processes responsible for rivalry are not at all confined to situations involving the separate presentation of different stimuli to the two eyes. To the same effect, Campbell and Howell (1972) and Campbell et al (1973) eliminated a number of possible factors that would have been specific to the alternations between superimposed red and green stimuli. Chromatic aberration and fluctuations in accommodation were rejected on two counts: (1) the occurrence of monocular rivalry between superimposed gratings was shown to be dependent upon the difference in their orientation (alternations are not observed until there is a difference of 15-20 degrees), and (2) presbyopic subjects and subjects who have had the ciliary and sphincter muscles paralysed with the application of 1% atrophine sulphate, observe the alternations normally. Campbell et al (1973) also eliminated explanations involving chromatic stereopsis and convergence by demonstrating that monocular rivalry may be observed under strictly monocular viewing conditions, i.e. with one eye covered.

Further evidence of the familial relation between these perceptual phenomena comes from an observation that was made in the context of Experiment 11. When the image of a narrow bar was made to move across the screen by passing a length of thin wire through the focal plane of the projector carrying the random field, there occurred a masking of the parts of the red figure behind which the bar moved. Grindley and Townsend (1965) reported the same "movement masking" phenomenon when the moving and stationary stimuli (both of

which were achromatic) were presented to opposite eyes. That these are instances of the same phenomenon is indicated by the further observation of two effects that were reported by these authors. First, the masking was primarily confined to those parts of the red figure lying away from the point of fixation, and second, tracking or following the bar as it traversed the screen prevented the masking of any part of the figure. MacKay (1960) has made a similar observation with respect to stabilized images, viz. that they may disappear when an object is moved across the visual field.

The results of a previous study would appear to contradict the present findings. Smith (1968) demonstrated that structured fragmentations of stimulus c (cf. Fig. 22) were sufficiently less common in binocular rivalry than in afterimage viewing to warrant the conclusion that the two phenomena involve different mechanisms. However, the value of 60% that Smith obtained for the percentage of fragmentations that are structured in afterimage viewing is particularly high. Evans (1965) presented the same stimulus as a stabilized image and reports a value of approximately 15% for the same parameter; which is comparable with Smith's value of 9.6% for binocular rivalry. The situation with regard to structured and unstructured fragmentations needs clarifying before the implications of Smith's results for the present thesis can be properly evaluated.

The occurrence of a monocular analogue (Atkinson, Campbell, Fiorentini and Maffei, 1973; Campbell and Howell, 1972; Campbell et al, 1973; Honisett and Oldfield, 1961; Sindermann and Luddeke, 1972) militates against explanations of binocular rivalry that are based on the concept of contralateral suppression (Fox and Check, 1972), particularly those explanations that assign a major role to the inhibitory convergence of monocular inputs at the striate cortex (Bishop, 1971; Jung, 1961). The reproduction of

typical fragmentation effects under conditions that do not eliminate the effects of small involuntary eye movements casts doubt upon explanations of stabilized image phenomena that rely solely upon some form of local (peripheral) adaptation. Moreover, it is unlikely that some less peripheral, less localized adaptation process contributed to the present findings. With the monocular rivalry experiment for example, it is difficult to imagine how such a process might cause the fading of the figure, but not of the parts of the pattern upon which it is superimposed. In the case of the movement masking, the moving bar adds just the sort of variation that would be expected to revive the image of a figure (cf. MacKay, 1960). We may ask, then, how the scheme outlined in Chapter 4 can accommodate the disappearance of images under stabilized viewing conditions and in rivalry, and how these phenomena, in turn, suggest refinements to the scheme.

6.3 The Complete Disappearance of an Image

It will be remembered from the scheme outlined in Chapter 4, that three different activating inputs to the catalogue of conditional expectancies are responsible for initiating the feedback matching process: (i) a shift in attention or orienting response, (ii) the initiation of a voluntary act, and (iii) the feedback disparity signal. Though special emphasis may be given to the elimination of the last category of input in discussions of stabilized images, the procedures normally employed also ensure, quite inadvertently, the elimination of the other two inputs. Thus, because the stimuli employed are normally unchanging, the matching proces (and more importantly in this instance, the matching process involved in the feedforward system, cf. Chapter 4) is quickly able to very accurately match the incoming information, particularly since the quasi-random effects of involuntary eye movements are also eliminated. In accordance with Sokolov's (1960) understanding of habituation, under such circumstances the system would be expected to habituate quite quickly, thus eliminating an orienting response as an activating input to the catalogue of conditional expectancies. That the system's ceasing to orientate is important in the disappearance of stabilized images, is suggested by Kolers' (1972) observation that if the subject's calf or thigh is "flicked" whilst the image is reported to have disappeared, it quickly reappears (dishabituates?). Kolers points out, that such stimulation is unlikely to cause the subject to move his eyes and hence disturb the stabilizing equipment. Apart from anything else, this observation suggests that processes other than adaptation are involved in the disappearance of stabilized images.

With regard to the elimination of the second category

of input signal, it may be noted that, for practical reasons (to avoid displacing the contact lens for example), the subject viewing a stabilized image is normally asked to refrain from making any voluntary eye movements. That this is an important prerequisite for image disappearance is indicated by the fact that under certain conditions images are likely to disappear simply with their steady fixation (cf. above). Moreover, an afterimage that has disappeared may be "brought back" by making a voluntary saccade. However, though the latter observation would appear to contradict any explanation of the image's disappearance that relies solely upon processes of adaptation, such an explanation has been protected by the suggestion that such an eye movement causes a change in intra-ocular pressure which serves to reactivate adapted receptors. This suggests that in order to clearly differentiate the present approach to stabilized images from the adaptation explanation, the subject should have his eye musculature immobilized and, whilst an image has disappeared, attempt to make an eye movement. Though the present scheme would predict the immediate reappearance of the image, the adaptation approach clearly would not. We see then, in passing, that though the theoretical framework of Chapter 4 is couched in rather general terms, it can lead to testable predictions that differentiate it from other approaches.

To return to the elimination of the various activating inputs, stabilizing an image most clearly contributes to the elimination of the last category of input, the feedback disparity signal. With the effects of involuntary eye movements eliminated, together with the fact that the stimulus is unchanging, very quickly the feedback matching process may accurately match the incoming sensory data. In this context then, it may be considered that the

function of involuntary eye movements (other than those comprising the orienting response) is to ensure the continuous existence of a feedback error signal to the system. It is interesting to compare the behaviour of the proposed system with that of the proportional class of negative feedback controller used in regulation. It is perhaps more than coincidence that if the error signal of such a controller is brought to zero, by whatever means, the output is also zero, since output is by definition proportional to error. In the present case a matching process is also being executed, and when equality between sensory input and expected input is achieved by means of a stabilized image, the system is denied any disparity information and hence one of the three actuating inputs.

The disappearance of rivalling images may be accommodated in the theoretical scheme in a similar manner (cf. Chapter 4). Thus, since a rivalling stimulus is necessarily unchanging, the system would be expected to habituate and be unable to derive an orienting input from the stimulus. Furthermore, it is an overlooked fact, that in order for rivalry alternations to be observed, subjects must refrain from making any eye movements and steadily fixate the stimuli. There is, however, the additional problem with rivalry, of explaining why both rivalling stimuli do not disappear completely and simultaneously. In answer, it will be remembered that a proposed prerequisite for rivalry is that the two stimuli should suggest incompatible models-to-be-matched. Consequently, there is always a stimulus to which the system is not habituated, and from which it may derive an orienting input to the catalogue of conditional expectancies. Thus, the matching process is maintained in rivalry because there is always a relatively novel stimulus to initiate an orienting response. Consistent with all this, Helmholtz (1911) and Breese (1899) observed that by continually shifting attention between

the different aspects of a monocular image, its dominant status may be maintained.

In summary, the scheme outlined in Chapter 4 assigns the complete disappearance of both stabilized and rivalling images to a failure to maintain an activating input to the feedback matching process. The difference between the two phenomena resides in the fact that since the catalogue of conditional expectancies can not simultaneously accommodate both rivalling stimuli, there is always an alternative stimulus to which the system is not habituated and from which it is capable of deriving an orienting input.

6.4 The Partial Disappearance of Images

Focusing on the partial disappearance (fragmentation) of stabilized and rivalling images, there are two questions to be answered: (i) Why is a model of the world that does not incorporate all the sensory information selected in the first instance? (ii) How is it that such a model is not immediately disconfirmed by the feedback matching process?

The first question is difficult to answer though there are a number of possibilities within the scheme by which such an incomplete model may arise. First, Honisett and Oldfield (1961) suggest that the internal model of the world is in a constant state of flux, particularly in the absence of the stabilizing influence of an activating input. Second, the higher-order catalogue, whose function is to detect and store information about regular sequences of events, may select an incomplete model-to-be-matched in anticipation of change. In this way, this higher-order catalogue may be the factor responsible for the constant state of flux of the model-to-be-matched in the absence of other activating inputs.

Third, the feedforward mechanism may be sensitive to alternative interpretations of the sensory information, particularly after habituating to the stimulus as a whole, and may feedforward these interpretations to the catalogue. There are other, more complex ways in which different models-to-be-matched may be selected on the basis of the same sensory input. There is at this stage, however, no evidence that will allow any of these hypotheses to be evaluated.

Consideration of the second question proves much more fruitful, and indicates how the scheme outlined in Chapter 4 may be refined and further anchored to physiological parameters. It will be argued that an incomplete model-to-be-matched (corresponding to a fragmented image) may avoid disconfirmation in the same way that in binocular rivalry a model-to-be-matched that does not incorporate one of the monocular images also avoids disconfirmation. It will also be proposed that the same principles that are responsible for the structured fragmentation of an image contribute to the observed tendency in binocular rivalry for each monocular stimulus to behave as a unit.

Implied in the scheme outlined in Chapter 4 is the notion that the feedback matching process is selective in its sampling of sensory information. It was suggested therefore, that a rivalling stimulus may not contribute to perceptual experience (be "suppressed"), not only because it fails to influence the selection of a model-to-be-matched, but because the corresponding sensory information in the feedback receptor system (geniculo-striate system) is not sampled by the feedback matching process, and does not contribute to the disparity signal. Clearly then, the same principle may explain how the alternative

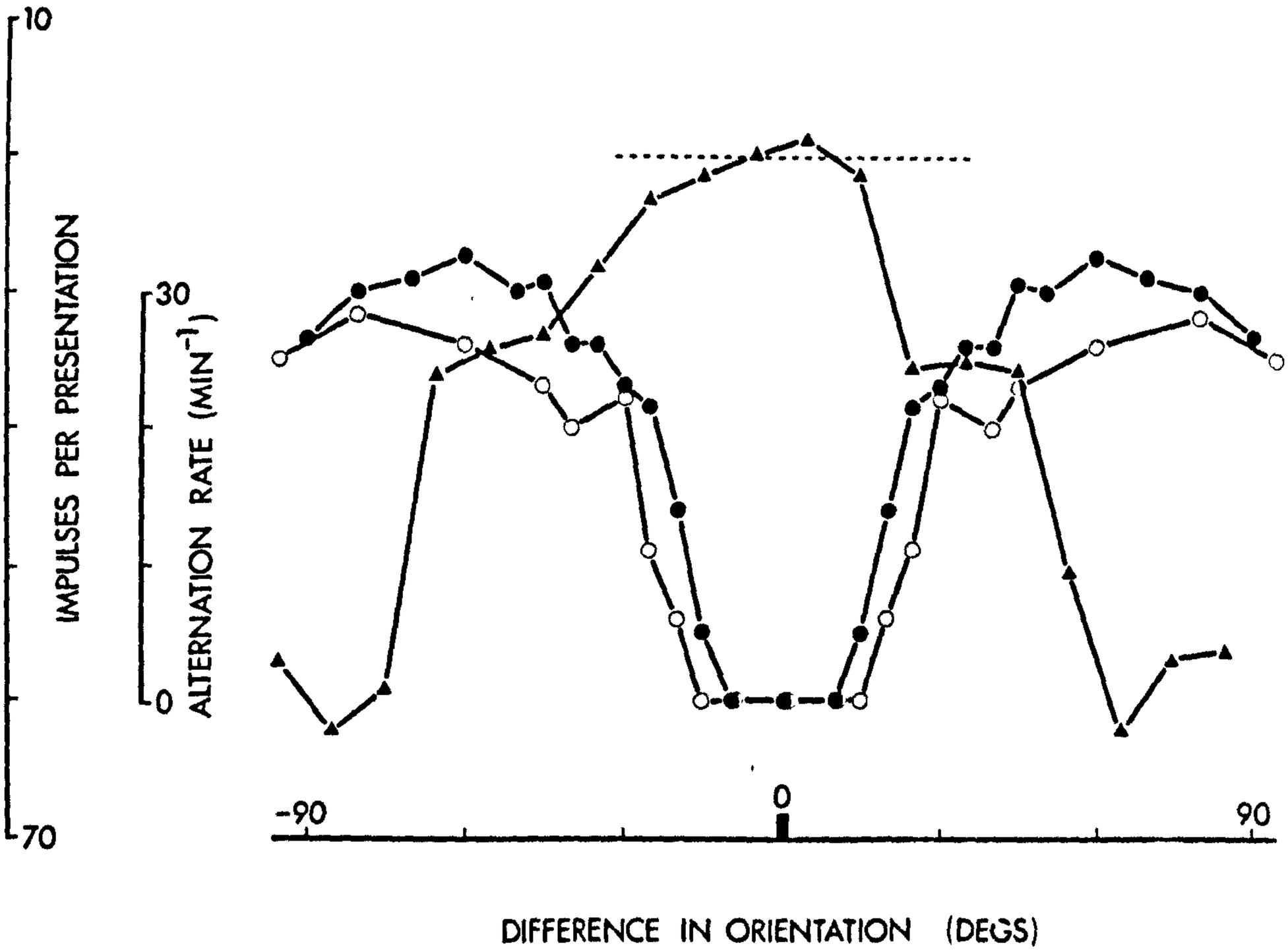
model-to-be-matched, that corresponds to a fragmented stimulus, manages to avoid being disconfirmed. We may go further than this, however, and ask why the fragmentation of images should be "structured", andwhy there is a tendency for the two monocular images in rivalry to behave in a unitary fashion. To this end, we may seek to reveal those aspects of visual cortex whose activity may be independently sampled.

6.5 Independent Physiological Channels and the Complete and Partial Disappearance of an Image

Campbell et al (1973) observed the change in the rate of monocular rivalry between two superimposed gratings as their orientations were made increasingly different. Finding that there were no alternations (neither image emerging as dominant) until the gratings differed by 15-20 deg., and that the rate of alternation then increased steadily until a ceiling was reached with a difference in orientation of about 60 degs., they suggested that "if two separate, and not significantly overlapping, populations of neurones are activated by the gratings, then alternation can occur" (p, 125). Whilst Campbell et al appear to define neurones as separate if they are incapable of responding positively to the same stimulus, a more appropriate definition, particularly in view of the fact that the rate of alternation did not reach a ceiling until there was a difference in orientation of 60 deg., perhaps involves the absence of lateral inhibitory connections. Thus, there appears to exist a negative correlation between the readiness with which two images display monocular rivalry, and the extent to which we may assume that there are lateral inhibitory processes between the corresponding neurones. It may be

Figure 26

Physiological data from cat visual cortex (▲). A complex cell's response to a high contrast bar that is optimally oriented and moving back and forth is plotted as a function of the orientation of a background grating. The dashed line indicates the mean level of spontaneous activity of the cell in the absence of the bar. Note the inversion of the ordinate (from Blakemore and Tobin, 1972). Data from two human observers (● and ○). The rate of monocular rivalry alternation between differently oriented gratings is plotted as a function of the differences in their orientation (from Campbell, Gilinsky, Howell, Riggs and Atkinson, 1973).


10
70
IMPULSES PER PRESENTATION
30
0
ALTERNATION RATE (MIN^{-1})
-90
0
90
DIFFERENCE IN ORIENTATION (DEGS)

noted that whilst the rate of alternation might appear to have nothing to do with the disappearance (suppression) in rivalry, it is the case that those conditions which yield the most distinct "suppression" of an image, also yield the more rapid alternation rate (Rauschecker, Campbell and Atkinson, 1973; Wade, 1975). Illustrated in Figure 26 are physiological data from visual cortex of cat, reflecting the presence of mutual inhibition between edge detectors having slightly different preferred orientations, and the data from two human observers who reported the monocular rivalry alternations between differently oriented gratings. Taken together, the functions suggest that the readiness with which two figures rival is negatively correlated with the magnitude of the inhibition effects between the corresponding neural channels.

To extrapolate, this relationship suggests that some "higher" mechanism in the visual system may confine itself to the sensory information regarding just one of two features (say), only to the extent that their presence is signalled by independent channels (populations of neurones). In terms of the model outlined in Chapter 4, therefore, it may be suggested that it is only to the extent that different stimulus features are signalled by independent neural systems that the feedback matching process may be selective in its sampling of sensory data provided by the geniculo-striate system.

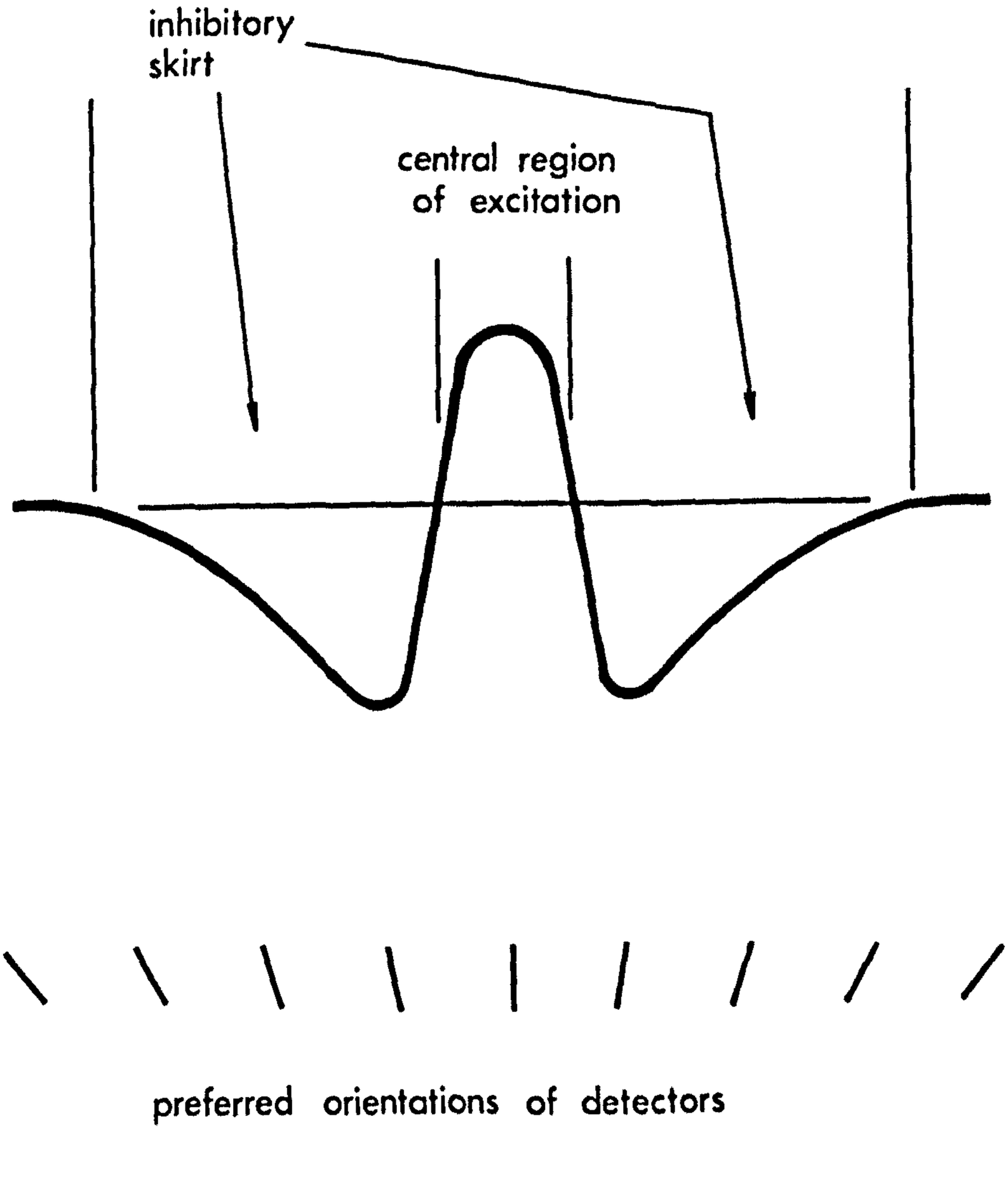
In the context of a sampling mechanism, it is particularly meaningful that the independence of neurones should be to some extent determined by the absence of lateral inhibitory processes, rather than simply by their inability to respond positively to the same stimulus. Consider an array of orientation-sensitive line detectors, whose preferred orientation gradually shifts as we consider each successively. Then with the presentation of a line

the distribution of activity that results incorporates a central region of excitation surrounded by a "skirt" of inhibition (cf. Figure 27, derived from Carpenter and Blakemore, 1973). It is imagined that some more centrally placed mechanism in the visual system, whether it be a more complex collector cell or some active sampling mechanism, monitors the levels of activity in such an array in order to determine whether a line of particular orientation is present within the visual field. The difference between Campbell et al's definition of independence, and the stricter definition involving lateral inhibition, reflects itself in the different ways by which such an higher-order mechanism might decide whether there is sufficient evidence that such a line exists. The first possibility is that the mechanism monitors the level of activity in the central region of excitation alone, and makes a decision as to whether a line is present on the basis of the difference between this level and the expected level of spontaneous activity. According to this first possibility then, the activity of neurones outside this rather limited central region of excitation will not influence the decision, and to this extent may be ignored by the higher mechanism. This is the possibility implied by Campbell's definition of independence.

According to the second possibility, the higher-order mechanism makes use of the existence of the skirt of inhibition that surrounds the central region of excitation in deciding whether a line of particular orientation exists. In this way, the level of activity of the central region of excitation need not be compared with some stored information concerning the expected level of spontaneous activity (which would be inefficient if this level were to vary at all), but rather with the surrounding level of activity. For this scheme, then, the activity level of other detectors may not influence the decision that a line of a particular orientation exists only to the extent that their preferred orientations ensure that they are outside

Figure 27

The distribution of activity, within an array of orientation-sensitive detectors, resulting from the presentation of a vertically-oriented stimulus.


inhibitory
skirt
central region
of excitation
preferred orientations of detectors

the range of the inhibitory skirt. This is the possibility that the stricter definition of independence implies, and it is consistent with the organization of the visual system at more peripheral levels.

To summarize, the significance for rivalry of the independence of two physiological channels may reside in the fact that the sampling of sensory information by the feedback matching process may be confined to one channel (stimulus), with the information transmitted in the neglected channel thereby failing to contribute to the disparity signal. In this way, a model-to-be-matched that does not incorporate all the incoming sensory information may avoid being disconfirmed.

Explanation of the structured fragmentation of rivalling and stabilized images may also be sought in terms of the sampling of sensory information that is signalled by a subset of the independent physiological channels engaged by a stimulus. Thus, we may define those "meaningful" components or elements of a stimulus that disappear independently of each other by referring to the absence of lateral inhibitory processes between their respective channels, and this would explain why the fragmentation of images is anything but randomly determined. It would also readily explain why angular figures fragment more readily than curved figures, and why, in binocular rivalry, the two monocular images tend to behave in a unitary fashion. One need only assume that lateral inhibition between neurones is largely confined to those monocularly driven neurones deriving their input from the same eye, and evidence to support this will be presented in later sections.

Though Atkinson (1972) has assigned a rather different role to lateral inhibition on the basis of the effects that the presence of a second afterimage has on the visibility of a first afterimage, two features of this study must be noted. First, Atkinson was not concerned with the extent to which the two stimuli behaved independently, i.e. with structured fragmentation per se. Second, the orientation specificity of the interaction between the two afterimages was wrongly interpreted. With two bars as stimuli, Atkinson found that they disappeared much more readily when their orientations differed by 45 and 90 degrees, than when their orientations were the same or they were observed individually. However, this may not be explained by lateral inhibition between orientation-sensitive channels as Atkinson suggests. On the contrary, for differences in orientation of 45 and 90 degrees, lateral inhibition between the respective neural channels is weak, and in the latter condition probably non-existent (Blakemore, and Tobin, 1972; Carpenter and Blakemore, 1973).

6.6 Evidence that an Image will "Suppress" Another only to the Extent that the Physiological Channels they Engage are Independent.

The notion that a prerequisite for rivalry "suppression" is the selective stimulation of independent channels is in complete contrast to the view that rivalry reflects the reciprocal inhibition of the two monocular channels (cf. Chapter 2, and more recently Abadi, 1976; Wade, 1975c). It is important therefore, to enquire whether there is additional evidence to support this notion. In doing so, it may be asked if rivalry suppression is more likely to

occur, and is more distinct, when increasingly independent physiological channels are selectively stimulated.

Monocular rivalry between differently oriented gratings is much more distinct, the alternations much more frequent, when one grating is coloured red and the other green (Rauschecker, Campbell and Atkinson, 1973; Wade, 1975a). Paralleling this, recent psychophysical observations have indicated that largely different populations of orientation detectors are responsible for representing this parameter as it relates to stimuli of different wavelength. Thus, the orientation aftereffect is largely colour specific, so that adapting to the orientation of a red grating has much less effect on the apparent orientation of a green test grating, than on a red test grating (Held and Shattuck, 1971; Lovegrove and Over, 1973; Broerse, Over and Lovegrove, 1975). The assumption is made that the effects of adaptation to a particular stimulus feature will be observed only to the extent that the test stimulus is represented by the detector mechanisms responsible for the adaptation stimulus (Over, Long and Lovegrove, 1973). Monocular rivalry is also much more distinct with strictly opponent colours (Rauschecker, Campbell and Atkinson, 1973; Wade, 1975a) which again implies that the degree of "suppression" is correlated with the extent to which the underlying neural channels are separate, since colour opponency within the visual system ensures that no neurones are able to respond positively to both opponent colours. Furthermore, consistent with the stricter definition of independence, it has also been observed that lateral inhibition is much less evident between feature detectors that are differently, rather than similarly colour-coded. Though this has only been demonstrated with reference to movement detectors (Over and Lovegrove, 1973) it has been suggested that this is a characteristic of all colour-coded feature detectors (Over and Lovegrove, 1973).

With the non-dominant grating disappearing completely rather than simply receding in to the background, the binocular rivalry between achromatic gratings is much more distinct than their rivalry under monocular conditions (Wade, 1975a). Confirming this difference is the observation that when stimuli that are sufficiently different for their fusion to be precluded are presented to the two eyes, the monocular channels they engage are independent; neither influencing the other in a positive (excitatory) or negative (inhibitory) way. This has been demonstrated by presenting animals with such stimuli for the entire period of their development, and noting the subsequent effects on the neural structure of the visual system. The underlying assumption is that those neural connections that are engaged by the stimuli in the normal animal will be the only ones to develop. Hirsch (1972), and Spinelli, Hirsch, Phelps and Metzler (1972) reared kittens with a horizontally oriented grating fixed firmly in front of one eye, and a vertically oriented grating in front of the other. The animals experienced no other visual stimuli. It was later discovered that there were no neurones in visual cortex that could be influenced by stimulation of either eye. The neurones capable of responding to information originating in the left eye were entirely separate from those capable of responding to information originating in the right eye. Ensuring in a rather different way that the two eyes receive different input, has produced similar results. Thus, Hubel and Wiesel (1965) induced an artificial squint in young kittens and observed that the neurones in visual cortex that developed any degree of response specificity were exclusively monocularly driven. Moreover, recent psychophysical observations have confirmed that people with a congenital strabismus fail to develop binocularly driven neurones; the two monocular channels remaining quite independent of each other (Mitchell and Ware, 1974; Ware and Mitchell, 1974; Movshon, Chambers

and Blakemore, 1972; Lehmkuhle and Fox, 1975). Interestingly, it is consistent with the hypothesis under discussion that the perceptual "suppression" of a monocular input is one of the characteristics of strabismus amblyopia. Indeed, in some cases of strabismus there is an alternation in dominance.

The data relating to strabismus confirm the notion that the neural channels engaged by the two stimuli in binocular rivalry are independent, and indeed, more independent than in the case of monocular rivalry. The fact that rivalry suppression is much more clear cut in the former case is, therefore, consistent with the notion that images may "suppress" each other only to the extent that they are signalled by independent physiological channels.

If we next compare monocular and binocular rivalry between differently coloured stimuli, it is observed that suppression is much more distinct , the disappearance more complete, in the latter condition. Paralleling this difference, recent psychophysical (Broerse, Over and Lovegrove, 1975; McCullough, 1965; Murch, 1972; Lovegrove and Over, 1973; Coltheart, 1973; Mayhew and Anstis, 1972 etc.) and physiological (cf. Coltheart, 1973) evidence indicates that colour-coded neurones are exclusively monocularly driven. Thus, consistent with the more complete suppression in binocular than monocular rivalry between different coloured stimuli (Wade, 1975) we see that the conditions of stimulus presentation in the former case serve to further segregate the neural channels engaged by the two stimuli.

In summary, there is evidence, other than than illustrated in Figure 26, to support the notion that the distinctiveness

of rivalry correlates with the degree to which the neural channels engaged by the rivalling stimuli are independent. With this in mind, a continuum of effects may be suggested, ranging from the alternation of ambiguous figures to binocular rivalry, according to which the extent to which stimuli disappear may be correlated with the extent to which the underlying set of physiological channels engaged by the stimuli are independent.

extent to which the non-dominant image disappears

→

extent to which the neural channels engaged by the two images are independent

→

the alternation of ambiguous figures → monocular rivalry between → binocular rivalry between

monocular rivalry between:
- achromatic stimuli
- differently coloured stimuli

binocular rivalry between:
- achromatic stimuli
- differently coloured stimuli

6.7 Experimental Verification of the Significance of the Independence of Physiological Channels for Rivalry

The fact that the suppression of an image is much more distinct in binocular rivalry than in monocular rivalry would lead the stricter definition of the independence of neural channels to predict that lateral inhibition between feature detectors is primarily confined to those monocularly driven detectors that derive their sensory input from the same eye, and does not occur between monocularly driven detectors that derive their input from opposite eyes, or between binocularly driven detectors. This is not such a strange suggestion if it is assumed that the function served by lateral inhibition is the development and refinement of the response specificity of neurones. One need only postulate that for such fundamental parameters as stimulus movement and orientation the response specificity of neurones is established before the level at which the two monocular channels converge. That lateral inhibition between certain feature detectors is confined to those monocularly driven detectors that derive their input from the same eye is, then, the prediction of the stricter definition of the independence of neural channels, and to confirm it would be to add greatly to the credibility of the definition itself, and to the credibility of the theory developed in the preceding section concerning the selective sampling of sensory information. Reported below are three investigations which offer a preliminary test of this prediction as it relates to stimulus movement and orientation.

6.7.1 EXPERIMENT 13 LATERAL INTERACTION BETWEEN NEURAL CHANNELS SENSITIVE TO VELOCITY IN THE HUMAN VISUAL SYSTEM [1]

MacKay (1973) made use of the phenomenon of simultaneous contrast to provide evidence for the existence in the human visual system of neural channels sensitive to the density of visual texture and for the presence of lateral interaction between such channels. Important in the present context, however, MacKay failed to observe the texture density contrast effect when the different aspects of his display were presented to different eyes. This implied that lateral inhibition between texture density detectors is confined to those monocularly driven units that derive their input from the same eye. Thus, according to MacKay, "This suggests that the abstraction of texture density takes place at a relatively early stage in the neural processing of retinal signals, and that the lateral inhibitory mechanisms presumably responsible for these contrast enhancements are located mainly in the uniocular systems before binocular fusion" (op cit, p 161).

1 The author is indebted to Dr. D.J. Powell for writing the computer programme used to generate the visual display employed in these observations.

The phenomenon of simultaneous contrast suggested itself as a means of determining whether, or to what extent, lateral inhibition is similarly restricted in relation to other fundamental stimulus parameters, such as movement and orientation. Considering the first of these, the preliminary psychophysical observations of Pantle and Sekuler (1968) suggest that velocity-sensitive channels exist in the human visual system. These researchers demonstrated a luminance threshold elevation for moving contours that is limited to a range of values around the velocity of the adapting contour. The following observations looked for the existence of such channels in a rather different way, but more importantly focused on the lateral inhibition between them.

A 10 x 6 matrix of dots was generated on the CRT display of a PDP-12 laboratory computer. The ten symbols in each row were programmed to move at a constant velocity in a west-east direction, giving the impression of a continuous stream of dots drifting across a window. A sharp discontinuity (or border) was generated by having the upper set of three rows move at a slower speed than the lower set. Viewed from a distance of 0.8 m the rows and columns of the matrix subtended visual angles of 3 deg. and 1.88 deg. respectively.

With velocities fixed at 0.3 degree s^{-1} and 0.6 degree s^{-1}, for the upper and lower rows respectively, the author and several colleagues experienced an illusion that is consistent with lateral interaction effects. More specifically, the difference in velocity of the rows adjacent to the discontinuity appeared enhanced when compared with the corresponding difference between more outlying rows (for example, the top compared with the bottom row). Perhaps counter-intuitively, the regular columnar organization seemed to assist in the appreciation of the illusion; the

apparent differences in velocity being translated into noticeable deviations from this regularity.

In order to determine more precisely the perceived velocity 'profile' of the matrix, a probe, or comparison row of eight dots was added to one side of the display. Two parameters of this row were made variable: (i) its vertical position could be programmed to coincide with any one of the six rows in the matrix, and (ii) its velocity could be altered by repositioning a smooth lever. By matching the comparison row to each of the six rows of the matrix, an estimate of the perceived velocity profile could be obtained.

The author overcame the initial difficulties that were experienced in trying to both observe the illusion and match the velocity of a selected row and provided the profile illustrated in Figure 28a. For comparison, the same procedure was followed whilst the dots in all six rows moved with the same velocity, being in the one case 0.6 degree s^{-1} and in the other 0.3 degree s^{-1} (Figure 28b). A comparison of the different profiles highlights the simultaneous contrast character of the illusion.

Incorporated in Figure 28a, are the results that are particularly important in the present context. These were obtained from a condition that involved the presentation of the "fast" and "slow" moving rows to separate eyes (the left and right respectively). This was made possible by mounting two polaroid filters on the CRT display unit, such that their axes were orthogonal for the fast and slow moving aspects of the matrix, and by wearing specially constructed goggles that incorporated separate polaroid filters before the two eyes. That the illusion did not occur in this condition is consistent with MacKay's result

with texture density, and demonstrates that for velocity, as for texture density, lateral inhibition is confined to the monocularly driven units that derive their input from the same eye.

To summarize, these observations suggest that the human visual system incorporates neural channels that are selectively sensitive to the velocity of a moving stimulus, and that the lateral inhibition between such channels is confined to those monocularly driven neurones that derive their input from the same eye. This confirms the prediction of the theory outlined in previous sections, which incorporates the notion of independent neural channels.

The author has since become aware of a paper by Over and Lovegrove (1973) which reports very similar results. These authors observed the effects of the movement of a surrounding pattern on the perceived velocity of a surrounded pattern. They noted that the differences in movement between the two patterns was enhanced and assigned responsibility for this to lateral inhibition. When the surrounding and surrounded patterns were presented to separate eyes, however, the authors discovered that the illusion was greatly weakened, again implying that lateral inhibition between motion detectors is primarily confined to those monocularly driven neurones that derive their sensory input from the same eye.

Figure 28

Perceived velocity of each of the six rows in the matrix of dots, with each point representing the average of three observations. The vertical bars delineate the range of values spanned by the two extreme observations in each case.

a, ● , The perceived velocity profile obtained when velocities of 0.30 degree sec^{-1} and 0.6 degree sec^{-1} were assigned, respectively, to the upper and lower rows in the matrix. The profile adds confirmation to the illusion reported by several observers; ○ , with the fast and slow moving rows presented to separate eyes (the left and right respectively) simultaneous contrast does not occur. b, Profiles obtained in control trials in which all six rows were assigned the same velocity, being in the one case 0.6 degree sec^{-1} (▲) and in the other, 0.3 degree sec^{-1} (△).

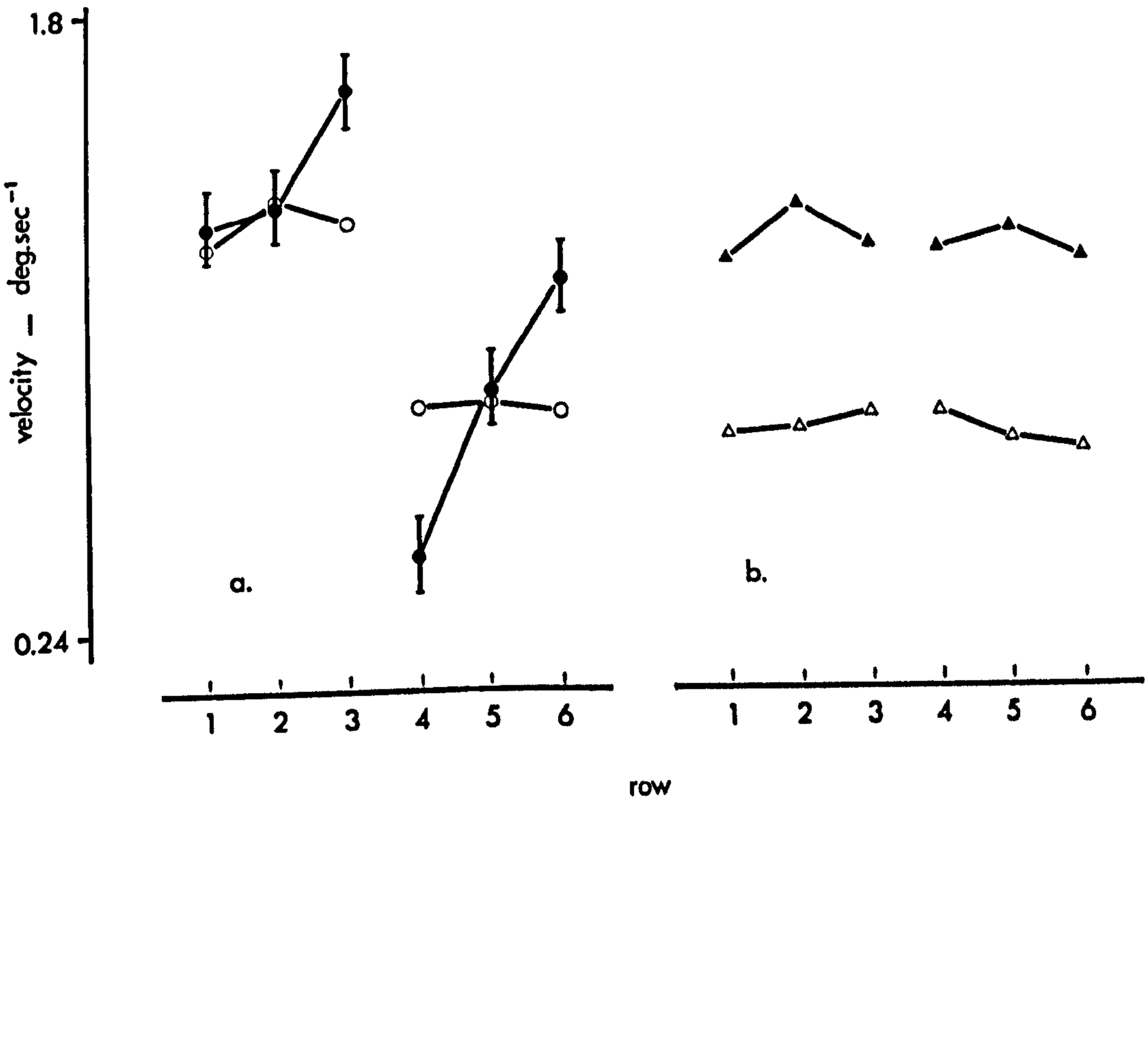

1.8
0.24
velocity — deg.sec⁻¹
a.
b.
1 2 3 4 5 6
1 2 3 4 5 6
row

Figure 29

The configuration normally used to illustrate simultaneous contrast, with the differing orientation of lines substituted for the usual variation in intensity.

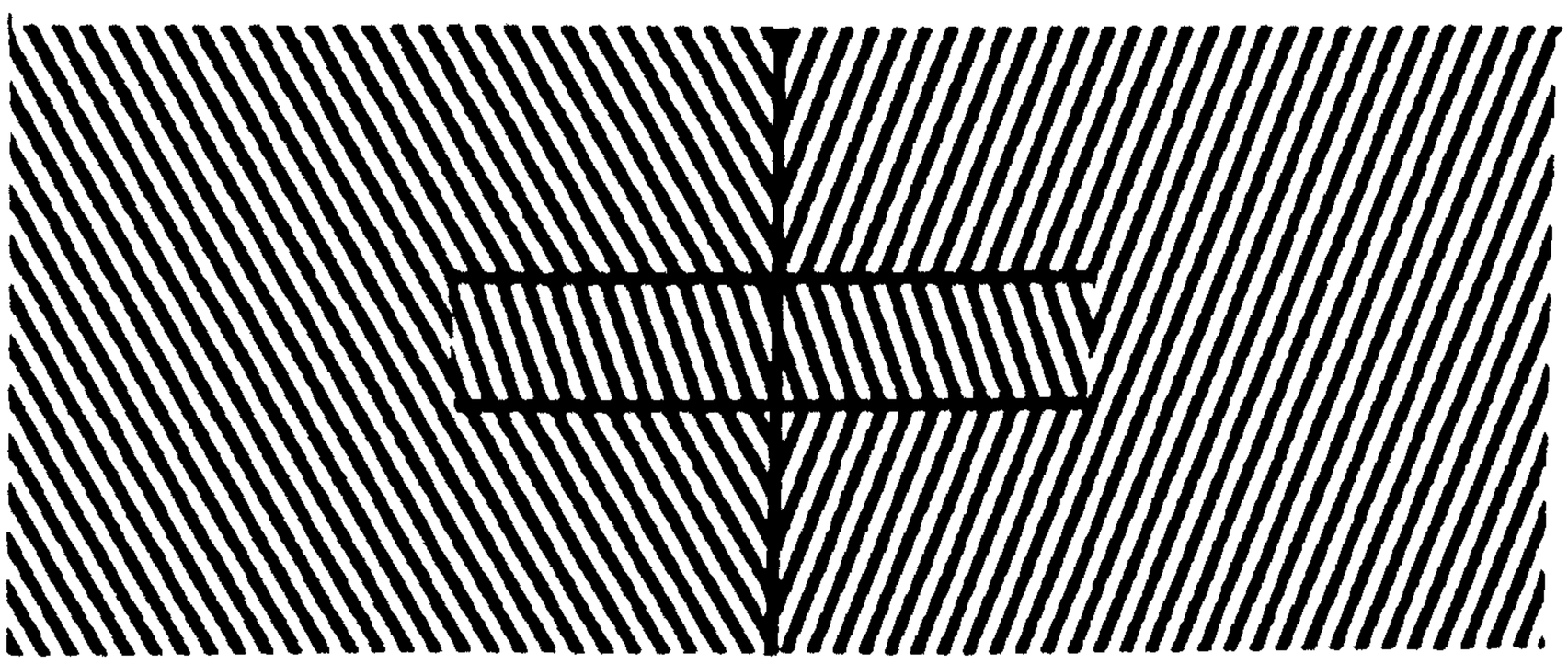
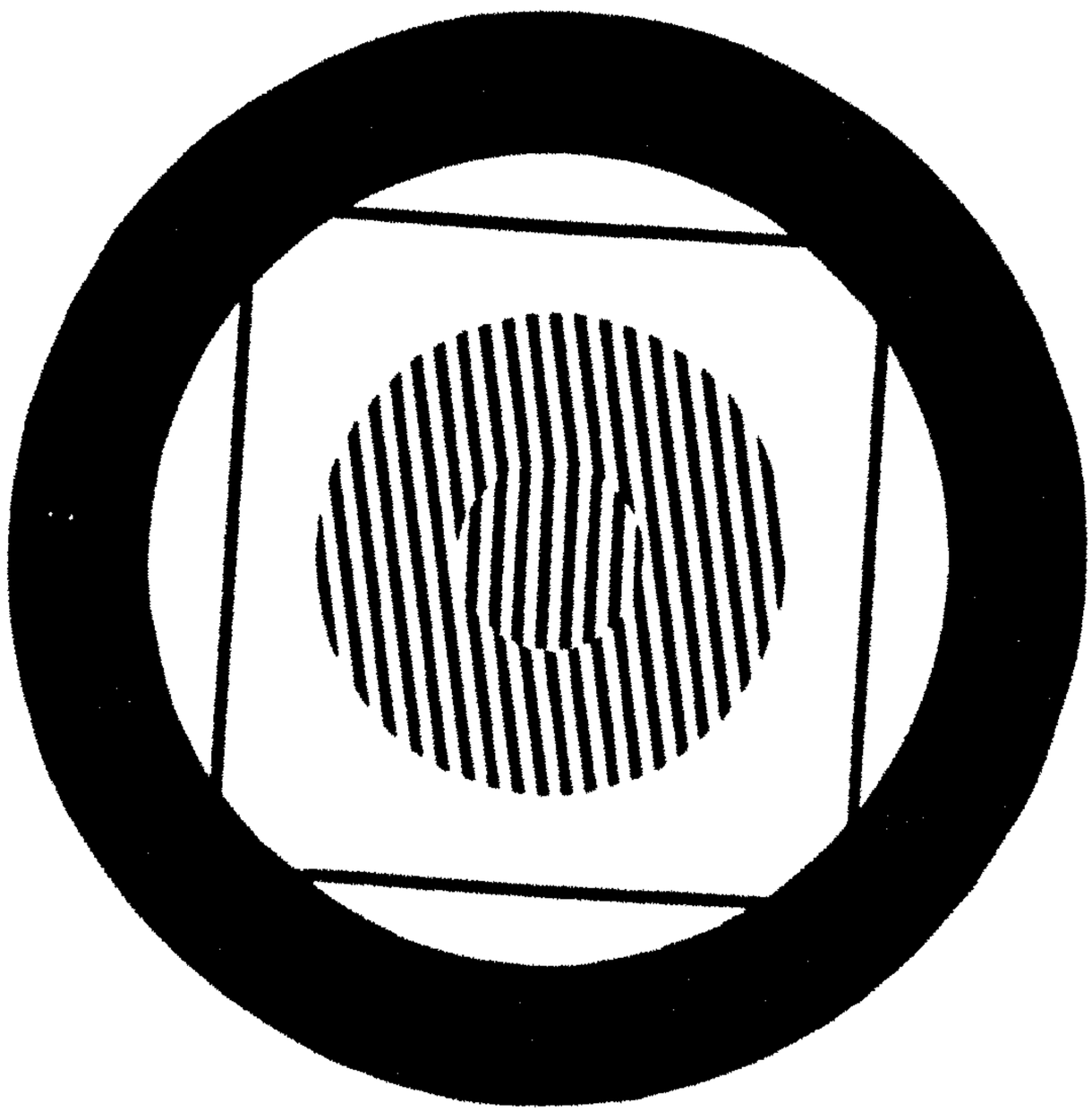


Figure 30

The format of the tilt illusion as seen by subjects in experiments 14 and 15. The inner grating is actually parallel to the vertical sides of the surrounding square.



6.7.2 EXPERIMENT 14 LATERAL INTERACTION BETWEEN ORIENTATION-SENSITIVE NEURAL CHANNELS

The phenomenon of simultaneous contrast may be used to test the same prediction with reference to stimulus orientation. Illustrated in Figure 29 is the configuration typically used to demonstrate simultaneous contrast, though here the differing orientation of lines is substituted for the usual variation in intensity. The fact that an illusion of altered orientation may be appreciated when the two halves of the central strip are compared, suggests that there exist orientation-sensitive neural channels in the human visual system and that there is lateral inhibition between these. Other authors have used different versions of this "tilt illusion" and provided evidence that it does indeed reflect the presence of lateral inhibition between orientation-sensitive channels (Andrews, 1965; Blakemore, Carpenter and Georgeson, 1970; Carpenter and Blakemore, 1973; Bouma and Andriessen,1970). As with the previous observations concerning velocity, the prediction under consideration may be tested by enquiring whether simultaneous contrast survives the dichoptic presentation of the different aspects of the illusion figures.

Insofar as a number of well known visual illusions, such as the Zollner, may be explicable solely in terms of the lateral inhibition between orientation-sensitive channels (cf. Carpenter and Blakemore, 1973) there have already been several attempts to test this prediction (cf. for example, Schiller and Wiener, 1962; Springbett, 1961; Day, 1961). Though all of these attempts have agreed in showing the near elimination of such illusions under dichoptic viewing conditions, interpretation has been hindered by the occurrence of a marked rivalry

between the two aspects of the illusion figures presented to the two eyes. To avoid this, a version of the tilt illusion was selected for investigation that did not involve the overlapping of the two parts of the illusion figures, as happens, for example, in the Zollner and Orbison illusions. For this reason, the version previously employed by Georgeson (1973) was adopted. In this, the perceived orientation of a centre grating is distorted by the orientation of a surround grating (cf. Figure 30). Thus, with a 5-30 deg. difference in orientation, the inner grating appears rotated from its true position, away from the outer grating. As will be mentioned, an additional advantage with this version of the tilt illusion stems from the fact that whilst some rivalry is experienced when these two gratings are presented to opposite eyes, for much of the time both are clearly visible. Moreover, only very rarely does the surrounding grating disappear, so that any reduction in the extent of the illusion under such viewing conditions can not be attributed to the disappearance of the inducing stimulus.

METHOD

Before each trial, the orientation of the outer grating was set at one of nine values ranging from 0-90 deg. counterclockwise from vertical, and the inner grating was offset from vertical by 10 degs., equally often in a clockwise and counterclockwise direction for each of these settings. The order of presentation of the trials was randomized between and within sessions.

Each subject completed the experiment under two conditions. In the first of these the two gratings were placed in separate channels of a four-field binocular tachistoscope and presented to the subject's right eye

(monocular condition). The circular surround and the fixed vertical reference lines were omitted from the field containing the smaller grating. In the second condition the two gratings were presented to different eyes (dichoptic condition), and to facilitate the fusion of the two fields the reference lines were incorporated in each display. When removed from either display in this condition, the gratings were replaced by an homogeneous achromatic surface of equivalent space-averaged luminance. The illumination of each channel of the tachistoscope was fixed at 1.5 log ft. lamberts for the lighter parts of each display.

Apparatus

Each grating was constructed by applying commercial Letraset to the white surface of small perspex discs that were mounted on the back-plates of a four-field binocular tachistoscope. The disc carrying the smaller grating was linked to the axle of a small reversible motor and a series of gears reduced its rotational speed to 2.3 deg. sec^{-1}. The disc carrying the surrounding grating was not mounted on a motor, but could be manually rotated about its centre. Only the discs carrying the gratings were positioned on the inside of the back-plates, and thus only they were visible to the subject. Fixed firmly to the axes upon which the discs were mounted, were aluminium pointers that travelled over a scale that was calibrated in degrees deviation from the orientation of the vertical reference lines. When the broken square that surrounded the outer grating was incorporated in a field of the tachistoscope, it was not fixed to the rotating disc, but rather to the back-plate itself.

The hand control of a Gaf automatic projector was linked to the motor that drove the smaller grating, in such a way that pressing the left and right buttons of the control served to drive the grating in a counterclockwise

and clockwise direction respectively. The length of cable attached to this hand control allowed the subject to comfortably view the stimulus display and at the same time rotate the inner grating.

The inner grating, outer grating, and the circular field within which they appeared, subtended 1.6, 4.8 and 8.0 degs. visual angle respectively. The lines themselves subtended 0.1 deg. visual angle.

Subjects

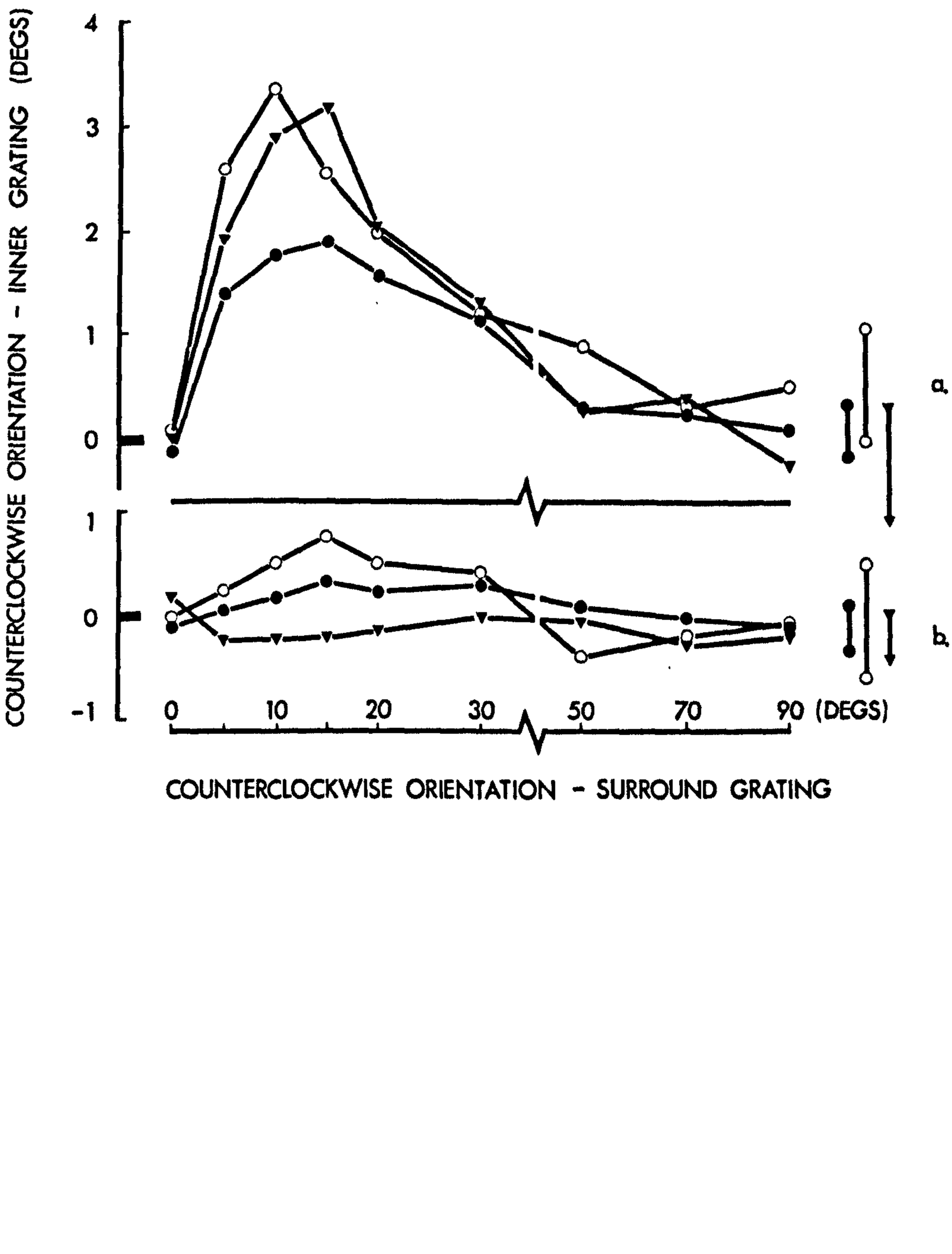
Two female undergraduate students who were ignorant of the purpose of the study, together with the experimenter, completed the experiment.

Procedure

Each subject was allowed a number of practice trials under both monocular and dichoptic viewing conditions, and with the surround grating oriented horizontally. Prior to the dichoptic trials, the subject adjusted the setting of the half-silvered mirrors to achieve binocular alignment. With the stimulus display continuously illuminated, the subject was instructed to ignore the outer grating and to rotate the inner grating, via the hand control, until it appeared parallel to the fixed vertical reference lines. Each setting of the motor-driven display took 45-60 seconds, and an interval of 30 sec. was allowed between each trial, during which subjects sat back from the tachistoscope. Six trials were undertaken by each subject, for each setting of the outer grating. The nine values chosen for the orientation of the outer grating are indicated in Figure 31.

Figure 31

For each position of the surround grating is shown the true orientation of the inner grating when this was perceived to be parallel to the fixed vertical reference lines. Each point represents the average of six observations, from subjects PW (●), HC (▼) and SD (○). The vertical bars delineate the range of values spanned by two average standard deviations. Note the change in scale for the more extreme positions of the surround grating.
a and b, results from the monocular and dichoptic conditions respectively.


COUNTERCLOCKWISE ORIENTATION - INNER GRATING (DEGS)
4
3
2
1
0
1
0
-1
0
10
20
30
50
70
90 (DEGS)
a.
b.
COUNTERCLOCKWISE ORIENTATION - SURROUND GRATING

RESULTS AND ANALYSIS

The quantitative results are illustrated in Figure 31, where the average degree of distortion in the perceived orientation of the centre grating is shown for each orientation of the surround grating. In the monocular condition (Fig. 31a) the obtained profiles are highly consistent with the known properties of orientation-sensitive channels (Carpenter and Blakemore, 1973; Morant and Harris, 1965; Campbell and Maffei, 1970; Held and Shattuck, 1971) illustrating that all three subjects experienced the tilt illusion in the usual manner. In contrast, the profiles shown in Figure 31b indicate that rather different results emerged from the dichoptic condition. Only for one subject does there appear to be any evidence of an illusion, and in this instance the apparent rotation of the inner grating was reduced from a maximum of 3.3 degs., obtained in the monocular condition, to only 0.75 degs.

DISCUSSION

In agreement with previous studies (Schiller and Wiener, 1962; Springbett, 1961; Day, 1961) these results indicate, at the very least, that an illusion that is probably explicable solely in terms of lateral inhibition between orientation-sensitive channels is very much reduced under dichoptic viewing conditions. Consistent with the predictions of the theory outlined above, when taken in conjunction with the stricter definition of independence, the results indicate that lateral inhibition between orientation-sensitive channels is primarily confined to those channels that derive their sensory input from the same eye.

These data explain why the Zollner illusion proves exceptional in being very much reduced, and indeed eliminated for the present author, when perceived in one of Julesz's random element stereograms (cf. Julesz, 1971). (Julesz did not produce any stereograms illustrating other illusions that might also be explained solely on the basis of lateral inhibition between orientation-sensitive channels). Since these stereograms focus on the behaviour of binocularly driven neurones, this result supports the present hypothesis.

6.7.3 EXPERIMENT 15 THE INTEROCULAR TRANSFER OF THE TILT ILLUSION AND THE RATE OF BINOCULAR RIVALRY

The notion that subjects may differ in the extent to which lateral inhibition between orientation-sensitive channels is confined to those monocularly driven neurones that derive their input from the same eye, not only suggests a very interesting hypothesis to explain some of the between-subject variation in the rate of binocular rivalry, but also suggests a way in which to further test the hypothesis that the readiness with which images rival is correlated with the extent to which they engage independent physiological channels. It will be remembered that the readiness with which two images rival reflected itself in the rate of alternation in dominance, and so according to this last hypothesis, there should exist a negative correlation between the extent to which the tilt illusion survives dichoptic presentation, and the rate of disappearance of the inner grating.* A further group of subjects provided data that permitted a test of this prediction.

METHOD

With relatively minor modifications in design, the preceding study was repeated with a further group of subjects. The modifications involved a reduction in the number of different settings of the outer grating, only the four settings, 0, 15, 25 and 90 degrees counterclockwise from vertical were used, and a reduction in the number of trials completed with each of these settings, from six to four.

* Thus, those subjects for whom the tilt illusion is most destroyed with dichoptic presentation (indicative of the independence of the two monocular channels) should report the more frequent disappearance (higher rate of rivalry) of the inner grating.

In addition to these trials, subjects were instructed to complete a further three trials during which they were instructed to steadily fixate the display and to report the disappearance and reappearance of the inner grating. For this purpose subjects were provided with a push-button for use with their right hand, and instructed to press this whenever and for as long as the smaller grating disappeared. During these trials subjects viewed the stimulus display under the dichoptic conditions, with the outer grating set at 15 degrees counterclockwise from vertical and the inner grating set at vertical.

Finally, the precaution was taken of ensuring that no subject lacked normal stereoscopic vision, since there is evidence to indicate that such subjects do not possess binocularly driven neurones (Mitchell and Ware, 1974; Ware and Mitchell, 1974; Lehmkuhle and Fox, 1975). To this effect subjects were asked to inspect some of the more complex stereograms provided by Julesz (1971).

Subjects

Twelve undergraduate students of psychology, in their first year of study, served as subjects. All were capable of appreciating the figures incoporated in Julesz's stereograms

Orientation of outer grating (degs)	Viewing condition: Monocular 0	Monocular 15	Monocular 25	Monocular 90	Dichoptic 0	Dichoptic 15	Dichoptic 25	Dichoptic 90	a.	b. 15
1	0	0.40	0.10	0.10	0.10	-0.12	0.15	-0.20	-0.07	9.7
2	0	2.12	1.57	-0.30	-0.80	0.08	0.03	-0.12	0.54	10.0
3	0	2.56	2.27	0.08	-0.92	1.08	1.13	0.78	1.15	6.0
4	0	1.77	1.17	0.62	0.48	2.20	1.20	0.23	1.85	8.7
5	0	3.40	1.75	-0.55	0.87	2.42	0.80	1.20	1.39	11.0
6	0	0.79	0.20	-1.08	1.20	1.00	1.68	1.05	-0.13	13.3
7	0	2.77	2.57	0.85	-0.07	-0.27	0.38	-0.17	-0.15	10.7
8	0	1.22	1.09	-0.25	-0.40	-0.35	-0.05	-0.40	0.05	9.0
9	0	4.00	1.82	1.15	-0.42	0.30	0.25	0.00	0.51	4.0
10	0	1.42	1.09	0.59	-0.15	0.15	0.08	0.00	0.23	7.0
11	0	3.25	1.72	0.62	1.33	2.00	1.13	0.36	1.16	1.0
12	0	1.95	1.50	0.20	0.90	1.30	1.28	1.00	0.35	8.3

subject

For each orientation of the surround grating is given the mean value for the counterclockwise orientation of the inner grating when this was perceived to be parallel to the fixed vertical reference lines. In the two right hand columns are given (a) values for the strength of illusion in the dichoptic condition (as defined in text) and (b) values for the mean number of disappearances of the inner grating reported in a 1-min. period.

Source	D.F.	S.S.	M.S.	F
Between subjects	11	16.51		
Within subjects	36	8.49		
C	3	3.88	1.293	9.3
C x subjects	33	4.61	0.139	
Total	47	25.00		

Results of analysis of variance applied to the results from the dichoptic condition given in Table 32.

The C factor represents the variation due to the orientation of the surround grating.

Table 33

RESULTS AND ANALYSIS

The raw data are presented in Table 32. For each subject and setting of the outer grating is given the mean setting of the inner grating when this appeared parallel to the sides of the broken square. Positive values indicate counterclockwise deviation from vertical.

The data from the monocular condition confirm those of the preceding study and conform to the known behaviour of orientation-sensitive channels. Thus, each subject experienced the tilt illusion. To make this particularly clear the results have been adjusted, by the subtraction of a constant from each subject's four mean values, so that the 0 deg. condition is given a zero value. With every subject displaying the predicted pattern of results in this condition, statistical analysis was unnecessary.

As anticipated, the results from the dichoptic condition were not so consistent. Not only was the illusion reduced, on average, to something like 30% its normal strength, but at least a third of the subjects failed to experience an illusion in this condition. However, Table 33 presents a summary of the analysis of variance relating to these data, and a multiple comparison test revealed that the 15 and 25 degree conditions yielded significantly higher values than the 0 and 90 degree conditions ($F=27.16$; $df=1,33$; $P<0.005$) indicating some interocular transfer of the illusion.

Also included in Table 32, in the two right-hand columns, are the values for the degree of distortion in perceived orientation of the centre grating and the mean number of disappearances of the smaller grating, as reported in the additional three trials. The former parameter was defined

as $(X_0 + X_{90} - 2X_{15})/2$, where X_0, X_{90} and X_{15} represent the mean values for the setting of the inner grating in the 0, 90 and 15 degree conditions respectively. When these two parameters were compared, it was found, as predicted, that they were negatively correlated (Kendall's Tau = 0.67; $P < 0.025$).

In summary, these results show that though the tilt illusion may survive the dichoptic presentation of the stimulus display it may be reduced to something like 30% its normal strength, thus confirming the hypothesis that lateral inhibition between orientation detectors is primarily confined to those monocularly driven neurones that derive their sensory input from the same eye. As in the preceding study, individual differences in the extent to which the tilt illusion survived its dichoptic presentation were observed, and for a significant number of subjects the illusion was eliminated. More importantly, however, it was confirmed that those individuals who most clearly observed the illusion in the dichoptic condition, reported the fewest disappearances of the inner grating. This provides good support for the hypothesis that rivalry suppression occurs only to the extent that the physiological channels engaged by the rivalling stimuli are independent i.e. not linked via lateral inhibition, and hints at a most intriguing manner in which the scheme outlined in Chapter 4 may accommodate some of the between-subject variation in binocular rivalry.

6.8 Summary of Part 3

In Chapter 5, an analysis of the stochastic properties of the rivalry alternations was reported. The results revealed a clear similarity with the reversal of ambiguous figures, and it was suggested that the same underlying processes were responsible for the alternations in the two contexts. This supported the scheme outlined in Chapter 4, which considered binocular rivalry to reflect fundamental perceptual processes that are not at all confined to situations involving the separate presentation of different stimuli to the two eyes.

In the present chapter, discussion has focused on the perceptual "suppression" that is involved in binocular rivalry, and again it was asked if, as predicted by the theory outlined in Chapter 4, this was an aspect of rivalry that could be observed in other contexts. The stabilized viewing of images was suggested as one such context, particularly in view of recent evidence which questions the traditional view that underlying processes of adaptation are primarily responsible for the disappearance of such images. Consistent with the notion that the processes underlying binocular rivalry are not at all specific to situations that involve the separate presentation of different stimuli to the two eyes, it was discovered that images disappear in a comparable manner when viewed as stabilized and rivalling stimuli. In turn, this result confirms the suspicion that adaptation is not primarily responsible for the disappearance of stabilized images, since with binocular rivalry there is no attempt to eliminate the effects of small involuntary eye movements. The further demonstration that the same images behave in a

similar manner in monocular rivalry, provided perhaps the most convincing evidence in support of the notion that the processes underlying rivalry are rather fundamental perceptual processes. Thus, for example, the fact that rivalry may be observed under monocular viewing conditions served most forcefully to question the traditional notion that binocular rivalry reflects the existence of reciprocal inhibition between the two monocular channels.

It was next asked how the theory outlined in Chapter 4 might accommodate the total and partial disappearance of stabilized and rivalling images. With regard first to their total disappearance, it was argued that the conditions of stimulus presentation involved in these two situations serve to preclude the various activating inputs to the catalogue of conditional expectancies. Since, in the proposed scheme, these inputs provide the essential impetus for the matching process, the output of which is identified with perceptual experience, it follows that to eliminate these would be to preclude perceptual experience. This was how the scheme accommodated the total disappearance of stabilized and rivalling images. With regard to the problem of why, in binocular rivalry, both images do not disappear completely and simultaneously, it was pointed out that because the non-dominant stimulus can not be accommodated in the model currently being matched, there is always an alternative stimulus to which the system is not habituated and from which it is able to derive an activating input to the catalogue of conditional expectancies.

Turning to the partial disappearance of stabilized and rivalling images, there were two questions to be

answered. First, "Why should the system entertain a model-to-be-matched that does not accommodate all the sensory information?". And second, "How is it that such a model is not immediately disconfirmed by the feedback matching process?". In reply to the first question, it was accepted that whilst the control system envisaged would in a number of ways be likely to generate alternative and incomplete models-to-be-matched, nothing more could be said at this stage. Consideration of the second question proved much more fruitful, indicating how the scheme outlined in Chapter 4 could be refined and further anchored to physiological parameters. It was argued that it was for the same reason that a non-dominant stimulus in rivalry fails to contribute to the matching process, that a model-to-be-matched that does not incorporate all the information about a stabilized or rivalling image escapes disconfirmation. It was proposed, therefore, that the disconfirmation of such a model is avoided because the discrepant sensory information is not sampled by the feedback matching process and does not contribute a feedback error signal to the system. It was further proposed that the feedback matching process may selectively sample the sensory information relating to one of a number of stimuli, only to the extent that this stimulus is signalled by a neural channel that is independent of those channels signalling the presence of the other stimuli. Put another way, it was proposed that an incomplete model-to-be-matched may escape disconfirmation only to the extent that the sensory information that it does not incorporate engages physiological channels that are independent of those signalling the presence of the sensory information that it does incorporate. A definition of independence was put forward, and defended, that involved the absence of lateral interaction between neurones, and it was argued that with such a definition the scheme could accommodate the structured nature of the fragmentation

of images, together with the difference in behaviour of angular and curved images. The implication of all this was the prediction that rivalry suppression would occur only to the extent that the physiological channels engaged by the rivalling stimuli are not only incapable of responding to the same stimuli, but are not related via lateral inhibitory processes. Whilst in sharp contrast to the traditional view that rivalry suppression involves processes of inhibition, psychophysical and physiological evidence was abstracted from the literature in support of this hypothesis. With this evidence, it was suggested that the same fundamental processes were responsible for a number of perceptual phenomena, ranging from the alternation of ambiguous figures to binocular rivalry, and that the different characteristics of these phenomena simply reflected the varying extent to which the "competing" visual stimuli engage independent physiological channels. Finally, three experiments were reported whose specific aim was to test this independent-physiological-channels hypothesis, as it relates to binocular rivalry. These experiments demonstrated that, with regard to such fundamental parameters as stimulus movement and orientation, lateral interaction between neurones is indeed primarily confined to those monocularly driven units that derive their sensory input from the same eye. In addition, the final experiment provided evidence to indicate how the scheme might begin to successfully explain individual differences in the readiness with which binocular rivalry is observed.

In conclusion, the contents of Chapters 5 and 6 have much to recommend the theoretical scheme outlined in Chapter 4.

6.9 Returning to the Negative Evidence

There are three studies, still to be reviewed, that have a most direct bearing on the issue that is central to this thesis, concerning the fate of suppressed information. Whilst these studies were available for discussion when the review (cf. Chapter 2) was prepared, it was thought that since they became available only after the experiments reported in Part 1 had been completed, it would be more meaningful to postpone their discussion until this point. It is also important to bear in mind that these studies are reported by Fox and his colleagues who, it will be remembered from Chapter 2, adopt quite a different position regarding binocular rivalry than the one developed in this volume, believing that rivalry suppression reflects a peripherally acting contralateral inhibition that ensures a more or less blanket suppression of monocular information. It is, therefore, particularly important that these workers have themselves provided evidence that, in contradicting their own theory, gives the best possible support to the present thesis.

Blake and Fox (1974a) presented a vertical and a horizontal square wave grating to the left and right eye respectively. The horizontal grating had a spatial frequency of 4 c/deg., a high level of contrast (70%) and was made to reverse its phase at a constant rate of 4 Hz. In contrast, the vertical grating did not reverse, and had a relatively weak contrast level of 3-9%. The authors were interested in whether subjects could respond to a suppressed stimulus, and except for the important control condition, adopted the paradigm employed in Experiment 7 (cf. Chapter 3). Thus, at the beginning of its dominant

(dominant condition) or suppressed (suppressed condition) phases they replaced the vertical grating with a slightly different grating and monitored the time taken for the subject to detect this alteration.

In their first experiment the spatial frequency of the vertical grating was initially set at 6 c/deg. and then changed to either 2, 4, 6, 8 or 10 c/degree! Not surprisingly, in the dominant condition subjects responded to the change, by releasing a key, within approximately 0.5 seconds. In contrast however, the latency to notice the change was of the order 1.3 - 5 sec. in the suppressed condition, with subjects first noticing the change at the beginning of the next phase of dominance of the field. From this increased latency in the suppressed condition, the authors concluded that subjects are unable to discriminate the suppressed stimulus, and that suppression reflects an indiscriminate or blanket inhibition of the monocular information at some relatively peripheral level. However, there are several aspects of their data which suggest that not only is this conclusion quite unjustified, but that their subjects did indeed respond to the change in the vertical grating <u>whilst it was suppressed</u>. Blake and Fox report that subjects first noticed the change at the beginning of the next dominant phase of the vertical grating, and so we may take the latency to detect the change as an estimate of the duration of the suppressed phase of this grating. In view of the relative strength of the two stimuli (note the much higher level of contrast of the horizontal grating, coupled with its continuous reversal) it is surprising that, in one of the suppressed conditions, the mean duration of suppression of the vertical grating was as brief as 1.6 - 2.4 seconds. With such an extreme difference in stimulus strength it is surprising that the vertical grating was ever dominant. These values for the mean durations strongly suggest

therefore that though the shift in spatial frequency did not induce an immediate return to dominance of the vertical grating, it did lead to an earlier shift in dominance than would otherwise have been expected. It is extremely unfortunate that Blake and Fox failed to report the mean duration of suppression of the vertical grating as derived from a control condition that did not involve any change in this stimulus (the control condition employed in Experiment 7). However, one may reliably infer from other aspects of their data that the mean duration of suppression of the vertical grating was, in the suppressed condition, less than would be expected had there been no change in this stimulus. Thus, though Blake and Fox report that under control conditions there were large individual differences in the mean duration of suppression of the vertical grating, these differences are not evident in the results from the suppressed condition, implying that the shift in spatial frequency exerted some unifying influence on the course of rivalry by reducing the duration of suppression. We have seen in Chapter 5 that there is a positive correlation between the values for the mean and variance of the dominance phase durations. More convincing than this is the fact that the results from their suppressed condition show quite clearly that the mean duration of suppression was dependent upon the spatial frequency to which the vertical grating was changed. Thus, for example, whilst the mean duration of suppression was approximately 2.0 sec. when the vertical grating was shifted from 6 to 2 c/deg., it was 4.1 sec. when shifted to 4 c/degree. This dependence upon the spatial frequency of the vertical grating clearly indicates that during its suppressed phase the spatial frequency of this grating was discriminated, albeit unconsciously.

In their second experiment, the vertical grating was replaced by an equivalent grating oriented at 45 deg. from vertical, and again Blake and Fox argue unjustifiably from the fact that in the suppressed condition the average latency to detect the change was increased from 0.38 sec. (observed in the dominant condition) to 2.05 sec., that subjects were unable to respond to the change. Again they fail to report the mean duration that should have been expected on the basis of a control condition that did not involve any such change. This is particularly important, since the duration of suppression would be likely to be considerably longer than 2.05 seconds.

Their third and final experiment suffers the same shortcomings. In this, Blake and Fox held constant the spatial frequency and orientation of the vertical grating, but either increased or decreased its contrast. Whilst the time to detect the change was only slightly increased in the dominant condition compared to normal viewing it was appreciably increased in the suppressed condition, particularly with regard to the condition involving the reduction in contrast. However, even in this condition, it seems likely that the mean duration of suppression of the vertical grating was reduced by the change in contrast. Thus, for one subject, the mean duration of suppression of the verticalgrating in this condition was only 1.58 seconds. As with their first two experiments, it would appear unjustified to conclude that subjects are unable to discriminate the change in the vertical grating in the suppressed condition simply on the basis of the increased latency to consciously detect this change.

To summarize, though Blake and Fox conclude from these experiments that rivalry suppression reflects the blanket

inhibition or blocking of a monocular channel at a relatively peripheral level, their results can be given quite the opposite interpretation, particularly with respect to the first experiment. Thus, though their subjects were not immediately aware of the change in the vertical grating in the suppressed condition, nevertheless the re-emergence of this stimulus as the dominant one occurred earlier than would otherwise have been expected. This mirrors the finding of Experiment 7, that was reported in Part 1. It will be remembered that in this experiment, when the vertical grating was reversed during its suppressed phase, though it quickly reappeared, subjects did not actually perceive the reversal. In discussing this experiment it was argued that it provided one of the most convincing demonstrations of unconscious perception, and the same may now be said of the experiments reported by Blake and Fox.

In two subsequent studies (Blake and Fox, 1975b; Lehmkuhle and Fox, 1975) Fox has himself provided evidence that is consistent with the present interpretation of his previous results. In these studies, it is reported that rivalry suppression has no effect on the growth of the threshold elevation aftereffect (cf. Blakemore and Campbell, 1969), the spatial frequency shift aftereffect (cf. Blakemore and Sutton, 1969) or the movement aftereffect. Thus, the parts of the visual system that are responsible for these aftereffects continue to adapt during the stimulus' suppressed phases. Since these parts have been identified with cortical mechanisms, the clear implication of these results is that a suppressed stimulus enjoys continuous cortical analysis. These two studies are entirely consistent with the experiments reported in this thesis, and in particular they indicate that it would have been surprising had a visually evoked cortical potential not been recorded to a suppressed stimulus in Experiments 4 and 6.

The importance of these studies for the present thesis can not be over emphasized. It is not just that they confirm the findings of the experiments reported in Part 1, but that they appeared after these experiments had been completed, and were reported by researchers who believed that rivalry reflects a suppression, in the real sense of the word, of the monocular channels at a relatively peripheral level via some form of contralateral reciprocal inhibition. These studies are most encouraging for the theoretical treatment of Chapter 4.

Finally, mention has yet to be made of a study that has a direct bearing on the issue central to Part 1. Somekh and Wilding (1973) confirm the findings of the experiments reported in this section by showing that whilst a word that is briefly presented to one eye may be masked by a brighter stimulus that is simultaneously presented to the contralateral eye, its meaning may nevertheless influence a subject's associations to the masking stimulus.

CHAPTER 7 RECAPITULATION AND FURTHER RESEARCH

7.1 Recapitulation

This thesis has provided experimental support for the notion that the processes underlying perception and attention are of an active and endogenous nature. By demonstrating that the "suppressed" stimulus in binocular rivalry continues to be fully analyzed, it is shown that conscious perceptual experience reflects processes that are over and above the analysis of sensory information* Thus, it was discovered that the course of binocular rivalry is sensitive to the structural content (Experiments 1,3,7 & 8), movement (Experiment 1), meaning (Experiment 3) and novelty (Experiment 3) of the suppressed stimulus. Consistent with this, support was obtained for the literal interpretation of Levelt's thesis (Experiments 1,3,7 & 8), which holds that it is the currently suppressed stimulus that takes precedence in determining the moment of rivalry alternation. Finally, it was demonstrated (Experiments 4 & 6) that the early components of the cortical evoked potential are unaffected by the suppressed status of the monocular stimulus, indicating the continued cortical involvement with a stimulus during its suppressed phases.

* These results accord with recent findings in the auditory domain, which show that a relatively sophisticated analysis is undertaken on information residing in an unattended channel (cf. Lewis, 1970; Corteen and Wood, 1972; MacKay, 1973).

This thesis has also revealed something of the nature of these active processes. Thus, with the mechanism responsible for initiating a shift in perceptual dominance being found capable of (i) responding to the non-dominant information in rivalry (even when this is otherwise subliminal) (Experiments 1 & 3) and (ii) demonstrating habituation (Experiment 3), the physiological structures involved in binocular rivalry were tentatively identified (Chapter 3). These structures were identified further when it was demonstrated that the behaviour of the later components of the evoked potential, unlike that of the early components, may be correlated with perceptual dominance in rivalry (Experiments 4 & 6). When these facts were considered in the context of existing physiological data, whilst at the same time adopting a control systems approach toward perception, a model of the psychological and physiological bases of perception and attention was outlined (Chapter 4). This model incorporates the notion that there are two visual systems having complementary functions. Whilst the superior colliculus-posterior association cortex system functions as part of a feedforward control mechanism, being particularly sensitive to unperceived/unattended information and responsible for initiating a shift in attention, the geniculo-striate cortex system contributes to a feedback control mechanism. The interaction between these two visual systems is considered to be the most direct correlate of conscious perceptual experience, reflecting the sampling of sensory information from the primary visual system in order that an internal model of the world may be tested. The scheme thus extends previous notions as to the function of the midbrain and related visual centres of the brain and adds to those existing approaches toward perception that regard it as a process over and above the analysis of sensory information (Gregory, 1966; Hochberg, 1970; MacKay, 1967).

In the final part of the thesis, the model was tested and refined. Thus, a fundamental implication of the model is that images should behave in a manner characteristic of binocular rivalry in situations that do not involve the separate presentation of different stimuli to the two eyes. Consistent with this, an analysis of the stochastic properties of rivalry alternations revealed a similarity between this phenomenon and the phasic reversal of ambiguous figures (Chapter 5). Similarly, it was shown that visual rivalry may occur under monocular (not dichoptic) viewing conditions, with the fragmentation here and in binocular rivalry showing characteristics normally associated with the stabilized image (Experiments 9,10,11 & 12). It was next discussed how the model could accommodate the total and partial disappearance of images in these different contexts, and it was hypothesised that information may be selectively sampled from a subset of the independent physiological channels engaged by a stimulus, where such channels are considered independent to the extent that they do not interact via lateral inhibition. In this way, it was possible to relate a variety of perceptual phenomena, ranging from binocular rivalry between chromatic stimuli to the alternation of ambiguous figures, according to the extent to which the neural channels responsible for the alternative percepts were related via lateral inhibition. Thus, it was proposed that a stimulus may disappear completely and independently of another stimulus only to the extent that the corresponding neural channels are independent. Since stimuli disappear very readily in the case of binocular rivalry, experimental support for this refinement to the model was provided with the demonstration that lateral inhibition between neural channels selectively sensitive to movement (Experiment 13) or orientation (Experiments 14 & 15) is primarily confined to those monocularly driven channels

deriving their sensory input from the same eye. Finally, it was shown how the model, and more specifically the notion that information may be selectively sampled from independent physiological channels, may begin to explain individual differences in the perception of binocular rivalry (Experiment 15).

7.2 Further Research

The scheme outlined in Chapter 4 emphasized the importance of the interaction between the posterior association cortex and primary visual cortex as the most direct neural correlate of conscious perceptual experience. Since this interaction is presumed to be bi-directional, seriously questioned is the traditional notion that association cortex simply continues the analysis begun by primary cortex, albeit integrating information from the different modalities. It is clear therefore, that to reveal the hature of this interaction, at a neurophysiological level, is a most important avenue for future research.

Discussion has been largely confined to the visual domain, and so an outstanding question concerns the extent to which the same scheme may be applied to audition. Are there two auditory systems having complementary functions in perception and attention? Whilst there is less information regarding this modality, the data that are available are encouraging. For example, Jane, Masterton and Diamond (1965) have provided evidence that the inferior colliculus makes a significant contribution to auditory selective attention in cat. Indeed, they go further and suggest that the inferior and superior colliculi have parallel roles. Also significant for the present thesis, Picton and Hillyard (1974) have studied the auditory evoked potential in man, and suggested that some responsibility for the generation of the late component (P300), that they associate with attention, must go to structures outside the primary auditory system. Considering the effects of attention on the evoked potential, they suggest that, "The stability of the early components of the evoked response would seem to indicate that auditory information is analyzed in the lemniscal or primary auditory system in much the same manner regardless of whether it is

attended or not. A secondary auditory system, imperfectly defined but probably comprising the reticular formation, medial thalamus and association cortex, is involved when further evaluation of the significance of this auditory information is required .... <u>The secondary system functions to compare input from the primary auditory system with memory models or templates of expected or significant stimulus alternatives.</u> Once a relevant or significant signal has thereby been recognized this decision is followed by appropriate percepto-motor sequelae. These sequelae, reflecting the contingencies of a response set mode of attention, are associated with the generation of the widespread P300 complex recorded from the scalp" (p 198, underscoring mine). This hypothesis, which is entirely consistent with the scheme outlined in Chapter 4, requires further investigation. Can the components of the auditory evoked potential, that may be attributed to the primary auditory system, be generated in the absence of awareness for the stimulus? In general then, it needs to be asked if there are two auditory systems having the same complementary functions as the two visual systems. What are the effects on humans of lesions in the primary auditory system? Will such patients be found to have a capacity for hearing, albeit unconscious, that is comparable to the visual capacity recently found in those blind patients suffering damage to the primary visual system?

Remaining with the notion of two visual systems, it will be recalled from Chapter 4, that there were features of the superior colliculus - posterior association cortex system that made it a likely candidate for the structure mediating subliminal perception. Some evidence for this was provided in experiments 1 and 3. With this in mind, it would be instructive to determine if the characteristics of the blind patient's visual capacity, that was attributed to the superior colliculus - posterior association cortex (cf. Chapter 3), that distinguish it from normal visual

perception, are also the characteristics of subliminal perception. For example, when Sanders et al (1974) asked their patients to guess the location of a briefly presented target (exposure duration of 3 seconds), they found that their response was correlated with the actual location of presentation, but only for actual locations within 30 deg. of the fixation point. Would this also hold for normal subjects when presented with a subliminal stimulus? And conversely, since it has been found that upon being presented with a word at a subliminal level, normal subjects respond to its meaning rather than to its structure (cf. Dixon, 1971), one might ask if this would apply to these blind patients, even for a stimulus that for normal subjects would be consciously perceived.

A very important task, still outstanding, is to consider the wealth of purely psychological data concerning the nature of perception and selective attention, and to see how well these accord with the scheme outlined in Chapter 4. Is the notion of two visual systems having complementary functions the optimum way of integrating this information? There are a number of findings, discussion of which is beyond the scope of this thesis, which do fit nicely in to such a scheme.

One of the most interesting ideas to emerge from the thesis, is the notion that sensory information may be selectively sampled from a subset of the independent physiological channels engaged by a stimulus, their independence being defined by the absence of lateral inhibition. It was suggested that the structured nature of the fragmentation of images may be explained by this hypothesis. To test this one might present, as a stabilized image, two straight lines forming an acute angle. Some measure of the extent to which the two lines disappear independently of each other may then be correlated with

their difference in orientation. According to the above hypothesis, the function relating these two parameters should mirror the function that relates the extent to which there is lateral inhibition between two orientation-sensitive channels and the difference in their preferred orientation. The same study could be undertaken with regard to the fragmentation of images in binocular and monocular rivalry.

Support for the hypothesis that sensory information may be sampled from a subset of the independent physiological channels engaged by a stimulus was provided in Experiments 14 and 15 with the demonstration that whilst in binocular rivalry images readily disappear, lateral inhibition seems to be primarily confined to the monocularly driven channels that derive their sensory input from the same eye. A further prediction from the hypothesis that would be worth testing, is that whilst the readiness with which monocular rivalry alternations occur between two differently oriented gratings is dependent upon the difference in their orientation, this is not the case for binocular rivalry. It also goes without saying that it would be extremely interesting to confirm, at the single cell level, that lateral inhibition between units sensitive to such fundamental parameters as orientation is indeed confined to those monocularly driven detectors that derive their sensory input from the same eye.

Finally, this "sampling" hypothesis has implications for a variety of perceptual phenomena, including visual masking. In particular, it may go some way to explaining the distinction between the two types of masking that occur, integrating masking (where the masked stimulus seems to be embedded or hidden within the masking field) and interruption masking (where the masked stimulus seems to be obliterated). Whilst the former only occurs when both

masked and masking stimuli are presented to the same eye, the latter arises when these are presented to different eyes. Could it be that interruption masking reflects the restricted sampling of information, as in binocular rivalry, and that, therefore, it occurs only to the extent that the physiological channels engaged by the two stimuli are independent? If so, then interruption masking should occur when the two stimuli are differently coloured, albeit presented to the same eyes.

These then, are some of the many questions that have arisen from this thesis. It is hoped that answers will be forthcoming and will serve to refine the theoretical notions that have been developed.

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